Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics

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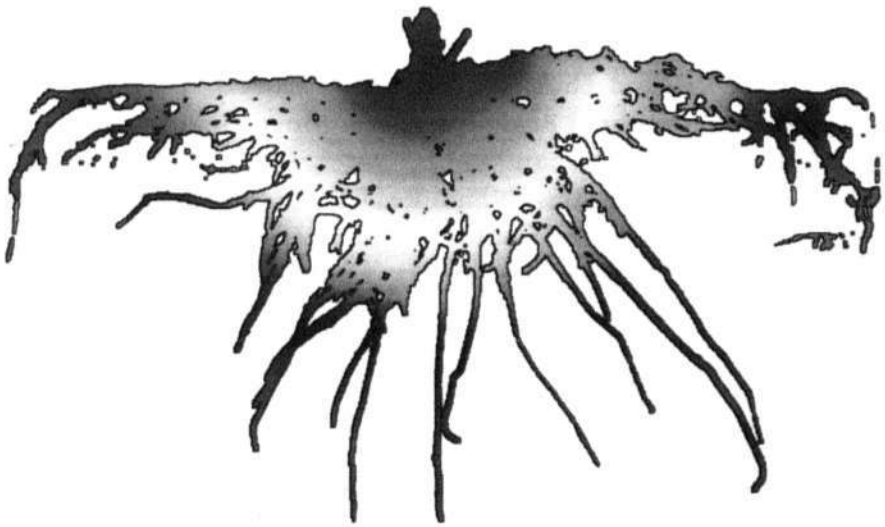

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Roots and nitrogen in cropping systems of the semi-arid tropics
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Foreword

Roots play important roles in plants, such as anchoring the plant and absorbing water and nutrients from the soil. Despite their importance, roots have been given little attention in field experiments due to their hidden nature below-ground and to technical difficulties in data collection. Nitrogen (N) has always been placed in the center of research projects in the semi-arid tropics because most soils in this region are N-deficient. Managing N in a given cropping system will have an immediate impact on crop productivity and profitability.

However, N has been seldom studied in relation to the root system under field conditions. In an intercropping system, where two different crops are grown in association, root interaction may significantly affect the crop growth through sharing or competition for the limited soil resources. This book is unique in that it describes roots and N from the viewpoint of cropping systems, focusing on intercropping.

Topics discussed are very important for agronomists and soil scientists to understand the recent developments in research on roots and N. The contributors have applied their deep knowledge and experience in cropping systems to basic aspects of roots and N. This book also provides comprehensive reviews on cropping systems, root system morphology, nutrient bioavailability, and root modeling.

Since its reorganization in 1993 (from the former institute, Tropical Agriculture Research Center, or TARC), the Japan International Research Center for Agricultural Sciences (JIRCAS) has allocated a great deal of its resources to root-related research, particularly that focusing on drought tolerance. It is now our firm belief that more detailed studies on root system morphology and function are necessary to increase agricultural production in areas where rainfall is not only low but also erratic.

The papers presented in this book cover a wide range of subjects. The information, I am sure, will prove useful to scientists working in these areas and will stimulate further interest in research on roots and N in cropping systems.

Nobuyoshi Maeno
Director General, JIRCAS

Foreword

This book is based on a Workshop held at ICRISAT Asia Center (IAC) during 21-25 November 1994, to mark the end of a Government of Japan (GOJ) Special Project, implemented through JIRCAS and conducted at IAC. The project, on nitrogen (N) dynamics of intercropping systems in the Semi-Arid Tropics (SAT), was conducted over five years, ending 30 November 1994. Drs O. Ito and R, Matsunaga were initially appointed as scientists on secondment to IAC, and they were subsequently joined by Dr S. Tobita as a post-doctoral fellow. Later, Dr Matsunaga was replaced by Dr K. Katayama, and Dr Tobita by Dr j.J. Adu-Gyamfi. The main findings from the considerable amount of research work undertaken during the project were presented and discussed at the Workshop. Also, the Workshop solicited views on the latest research advances from scientists with particular expertise in the subject matter covered by the project.

This Special Project followed an earlier project conducted during 1984-89. Under that project, Drs N. Ae, J. Arihara, and K. Okada, as scientists seconded to ICRISAT from the Tropical Agriculture Research Center (TARC, and now JIRCAS), Japan, studied phosphorus (P) nutrition of chickpea and pigeonpea in the SAT. Their research highlighted the role of root exudates of these pulses in releasing sparingly available P for uptake by these crops and its subsequent cycling in cropping systems. A workshop was held at the end of that earlier project, and a book prepared from the proceedings, entitled "Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics". These published findings of the initial project attracted the interest of those concerned with sustainability of cropping systems in agroecosystems where soil available-P levels are low and limiting. The success of the first GOJ Special Project also lead to implementation of the second one on N-dynamics. A third project began on December 1,1994.

The subject matter of the present book is reminiscent of that of a workshop held at ICRISAT in Hyderabad in January 1979 - The International Workshop on Intercropping. It is fitting that several participants in that Workshop are contributors to this book (e.g., Drs Trenbath, Snaydon, and Willey, and some long-serving ICRISAT staff members). The 1979 workshop focussed on describing the various forms of intercropping systems, the yield and economic advantages over sole cropping, and the above-ground interactions of intercrop components. However, R.W. Snaydon and P.M. Harris, in their paper in 1979, emphasized the role of water and nutrients in determining intercrop performance, and the need for research to determine how best to manipulate and improve the efficiency of use of these two resources. One question raised but not adequately answered in 1979 concerned the contribution of N fixed by the legume to the companion crop, within the season. This book allows us to reflect on progress made in knowledge of below-ground activitiy of intercropping systems in the SAT over the last 15 years, and in particular to see to what extent we can now answer questions raised long ago.

The publication of this book, and the holding of the Workshop from which it was

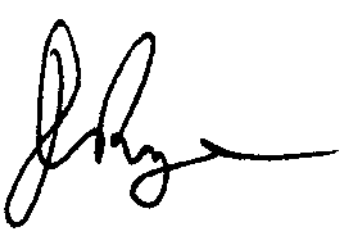
derived, coincides with a time when ICRISAT is embarking on a new mode of conducting research. It is therefore an appropriate time to reflect on past research efforts so as to best be able to prioritize future research investments. To implement the Medium Term Plan (MTP) for 1994-98, ICRISAT has been through an intensive change process involving:

- prioritization of some 110 research themes that formed the basis of our MTP proposal to our stakeholders
- restructuring of the organization and management into a matrix mode for research and related activities
- development of a production systems concept to assist us in improving the focus of our research towards eventual impact
- packaging of research themes into a new portfolio of 22 global research projects

Externally funded special projects such as the current GOJ Special Project are integrated into the new ICRISAT project portfolio, so as to gain synergies for the benefit of all. Indeed the contents of this book are now guiding workplans in ICRISAT's new Integrated Systems Projects.

More generally, it is hoped that this book will provide an up-to-date assessment of knowledge on the dynamics of roots and nitrogen in cropping systems of the SAT, and indicate appropriate directions for future research endeavors in this subject area.

James G. Ryan
Director General, ICRISAT



Preface

This book is based on papers presented at the International Workshop on "Dynamics of Roots and Nitrogen of Cropping Systems in the Semi-Arid Tropics", held at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Asia Center (IAC) 21-25 November 1994. The workshop was organized to share research results from Phase II of the Government of Japan (GOJ) Special Project and to solicit presentations from other research scientists actively involved in the area of roots and nitrogen (N) dynamics in cropping systems. The workshop was co-sponsored by Japan International Research Center for Agricultural Sciences (JIRCAS) and ICRISAT where the project was executed. There were 53 participants from 12 countries, and 42 scientific papers were presented along with 5 papers on the future research needs in the subject matter for each session of the Workshop. However, this book is not only intended to reproduce the presentations made at the workshop, but also to provide the latest information on dynamics of roots and N in cropping systems. For this reason, several more papers were added, and considerable re-writing and re-arranging of the original manuscripts were requested from each author.

Phase II of the GOJ project was initiated on December 1989, following Phase I, which concentrated on "Phosphorus nutrition of tropical legumes". Scientists in Phase I focused on the rooting behavior of the ICRISAT mandate crops (pearl millet, sorghum, pigeonpea, chickpea, and groundnut) in relation to phosphorus (P) nutrition. One of the most important findings from this phase was the identification of piscidic acid and its derivatives in root exudates of pigeonpea that enable the crop to absorb Fe-bound P.

Nitrogen is a major nutritional constraint that restricts productivity of crops in the semi-arid tropics (SAT). Due to the limiting N-supplying capacity of soil, leguminous crops should depend highly on N_2 fixation even though the N from fixation may be inadequate to satisfy their N requirements. A prerequisite to maximize productivity of leguminous crops is to increase the utilization of N from both soil and fertilizer, without affecting N_2 fixation by an external N supply. One approach is to have a better understanding of N flow into plants through symbiotic N_2 fixation and combined-N uptake from the rhizosphere.

During Phase II of the project, much effort was devoted to drawing an overall picture of the profile-distribution of water, nutrients, root system, and root activities of ICRISAT mandate crops (except chickpea). With this approach, the GOJ scientists in collaboration with their ICRISAT counterparts, focused on the relationship between rooting behavior and N flow in pigeonpea-based cropping systems. At the latter stages of the project, an attempt was made to establish a simple root model using the field data of water and nutrient flows, distribution of root systems, N uptake, N_2 fixation, biomass, and yield.

Despite the volume of research on cereal /legume intercropping, considerable gaps remain in our understanding of the below-ground interactions and N dynamics of the system. A combination of cereals and legumes are recommended for obtaining potential yield from the cereals and for maintaining soil fertility with N input through biological N_2

fixation by the legumes in the SAT. Pigeonpea is considered to be a suitable component crop for intercropping in Alfisols of Indian SAT, because it is characterized by a relatively long growing period and a deep root system.

Among various options available at the farm level, fertilizer management is the most promising to achieve an immediate increase in crop production in the area where most of the farmers have no access to irrigation facilities. The objectives of the GOJ project were (i) to characterize rooting habits and N uptake efficiency of pigeonpea, (ii) to analyze the N-supplying capacity of soils during the cropping season, and (iii) to compare methods and timing of N fertilizer application in terms of land productivity and N-use efficiency with a view to making appropriate recommendations for N management in the pigeonpea-based intercropping.

Following the project framework described above, this book is organized into five sections. Section I, "Intercropping in Cropping Systems", highlights the significance of intercropping in various cropping systems, especially in pigeonpea-based intercropping, which is widely practiced in the Indian SAT. Section 2, "Root Dynamics of Cropping Systems", describes the functions and morphology of root systems, and their changes in relation to genotypes of crops and environmental stresses such as excess and deficiency of moisture and nutrients. Section 3, "Crop Nitrogen Economy", mainly focuses on N input from biological N_2 fixation in relation to its balance with carbon input and N uptake. Section 4, "Soil Nitrogen Dynamics", provides a basic knowledge on the status and dynamics of N in soils and the effects of long-term cropping systems on the N budget, and discusses effective ways of N management in intercropping. Finally, Section 5, "Modeling Dynamics of Roots and Nitrogen", deals with the latest development of models for root growth, and root interaction, crop growth, and N budget in intercropping and in entire farming systems.

It is our earnest desire that the results of studies conducted as a part of the GOJ project at ICRISAT and information provided in this book will give fundamental reasons for beneficial effects of intercropping and crop rotation, and will impact basic and strategic research on cropping systems in the SAT.

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This book would not have been possible without the support of several people. The enthusiastic participation of the contributors to this book was essential. We thank them for the work and time they devoted to the writing of the chapters and for the thoroughness with which they took into account our editorial and technical comments. The financial support from the Ministry of Foreign Affairs of the Government of Japan (GOJ) and ICRISAT allowed us to organize the workshop. We thank Dr. Hiroshi Nakano, Team Leader (GOJ Phase III Project) for allowing the transfer of money from the phase III budget to prepare this book. Special thanks go to Mr. S. Saigo, Mr. H. Matsuo, and Mr. M. Fukushima for their important role as the First Secretary of Japanese Embassy at New Delhi to bridge the GO] and ICRISAT. The project was financially managed in healthy conditions from the beginning to the end owing to thoughtful administration by the International Cooperation and Planning Division, Economic Affairs Bureau, the Ministry of Agriculture, Forestry and Fisheries of Japan. We also owe a debt of gratitude to Dr. K. Minami, Director, Environmental Resources Division, JIRCAS, for his valuable suggestions in the editing process. We are indebted to Ms. Y. Ogata and Ms. Y. Maeda, Cultio Cooperation for all the tasks involved in manuscript preparation in the layout and design of the book, and Dr. E. Whitby and Ms. N. Whitby, Chimera Technologies, for the technical editing of the manuscripts. The secretarial work by Messers R. Narsing Rao, G. Shinde, and Ms S. Merajunnisa is gratefully acknowledged. Finally, we thank all the staff of GOJ Phase II Project for their technical support.

Significance of Intercropping in Cropping Systems

M. M. Anders[1], M. V. Potdar[1], and C. A. Francis[2]

Abstract

We do not know when intercropping began nor why early civilizations fostered its use. Whether by design or accident, intercropping dominated early agriculture and is still practiced in many areas of the world. With the advent of "modern" agriculture, intercropping began disappearing from many areas. This shift was driven primarily by mechanization and specialization. Despite pressures to abandon intercropping, it has survived and flourished. Increasing interest in sustainability and environmental concerns have shifted attention back to intercropping as a means of better utilization of resources while preserving the environment.

The large volume of literature that involves intercropping can be divided into two categories. The first is a collection of descriptive papers on existing intercropping systems. This collection provides extensive information on what farmers do but very little insight on why. The second is an even more voluminous collection of production descriptions of intercropping. What the first lacks in "why", the second lacks in its utility to effectively improve intercropping systems.

Quantitative descriptions of productivity in intercropping systems began in ernest with extensive use of the Land Equivalent Ratio (LER). Modifications of this methodology have been proposed but are not extensively used. Attempts to understand overall production increases in intercropping systems have led to discipline-based studies involving resource use with little or no consideration of pest and disease constraints. Numerous studies have demonstrated improved sunlight utilization in intercropping systems. Efforts to better understand the below-ground dynamics and nutrient utilization in intercropping systems are less numerous and have conclusions based on indirect measurements. Understanding these dynamics will improve our knowledge of why intercropping systems are more efficient and productive; but will this understanding lead to improved systems? We would be well advised to remember that, with rare exceptions, previous work has been carried out on research stations using designs and cropping mixtures seldom used by farmers. It is not known if the problems addressed in these studies actually represent farmers' constraints; thus, intercropping research has, for the most part, become "solution driven." We must be aware of this in our deliberations and seek to identify avenues of research that will result in real

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improvements in the systems we are studying.

History of intercropping

Andrews and Kassm (1976) state that intercropping is "growing two or more crops simultaneously on the same field. Crop intensification is in both the time and space dimensions. There is intercrop competition during all or part of crop growth. Farmers manage more than one crop at the same time in the same field". Intercropping is a practice quite possibly as old as settled agriculture. We may never know how the first "real" intercropped field appeared, but historians (Baker 1970; Chang 1983; De Wet et al. 1975; Harlan et al. 1976; Rindos 1984; Turner and Miksicek 1984) assure us that intercropping probably existed early in agricultures evolution. What we have been able to establish is that intercropping is part of a process of species domestication. Plucknett and Smith (1986) summarize this process and indicate the second stage of domestication as "protection of preferred plants" that resulted in the protection of wild plants along trails and around camps. This stage was followed by "gardening" that was a conscious planting or transplanting of wild species in a specific area. From this activity over many centuries evolved commercial farming as we know it today.

Despite formidable difficulties in establishing the exact times when intercropping appeared in the form of mixed garden plots, it has been established that such gardens were widespread throughout the world during Paleolithic times (Plucknett and Smith 1986). The process of evolving to formal mixed garden plots did not occur quickly but can be regarded as a gradual process extending back to Paleolithic times.

Information on exactly which cultigens were planted and where these first cultivations took place are questions that remain unanswered. It has been argued (Sauer 1969; Johannessen 1970; Gade 1975) that organized intercropping first occurred in areas where root crop agriculture was predominant. The reasoning is that root crops can be easily propagated by cuttings or corms, thus maintaining cultigen purity in humid tropical areas was relatively simple.

Cereals and pulses were not easily domesticated and have a long history of crossing with related wild species, usually considered as weeds. Many of the cereal and pulse crops have evolved from wild species which are, even today, found mixed with domesticated cultivars. We must thank our predecessors, farmers and biologists, for allowing, and in some cases promoting, weedy fields. Crops such as rye *(Secale cereale),* oats (*Avena spp.*), amaranths (*Amaranthus hypochondriacus and A. cruentus),* chenopodium (*Chenopodium nuttaliae*), beans (*Phaseolus spp.*), squashes (*Cucubita spp.*), and maize (*Zea mays*) evolved from weedy gardens (Wolf 1959; Sauer 1969). Whereas some farmers choose to not remove certain weed species (Wilkes 1977) that might enhance cultivated species production, breeders look to early cultigens for resistance to specific pest and disease problems. The goals of these two plant selection systems may or may not be the same, but it is in these somewhat divergent laboratories that our future genetic resources will evolve.

Intercropping activities have historically been identified in many parts of the world, e.g. cereal mixtures in temperate regions (Francis 1986). Intercropping is especially

important and continues to be widely practiced in the tropics. There is extensive natural genetic diversification in both crops and systems found in these areas (Lathrap 1970; Harris 1971; Eden 1974). Frequency of farmer use of intercropping decreases as temperature and rainfall decrease (Harris 1976). This trend is the result of fewer plant species being adapted to harsh growing conditions and farmers' favoring species that have a better probability of producing something in a bad year.

With the advent of modern agriculture, intercropping began to disappear from many industrialized countries. This trend was driven by mechanization and specialization. Crop species and cultivars were viewed as isolated components of the system in which they were grown, and research was centered on individual commodities. Specialization was considered the best strategy for increasing crop production. This may have been successful with single commodities, however, the question of improved system production remains unanswered.

Descriptions of intercropping systems

Interest in systematic studies on intercropping was first expressed by botanists studying plant communities and by social scientists studying food systems (Carneiro 1961; Conklin 1957; Rappaport 1968). These studies were not concerned with the efficiency of intercropping systems, but rather they described existing plant species and their frequencies. Numbers of plant species found in some areas were substantial. Eden (1980) described small gardens in the Colombian Amazon containing 5 to 18 cultivated species. These tropical gardens are multi-storey in nature and may be planted in geometric patterns (Cowell 1974).

The plant species used in intercropping can vary across regions and with specific gardens within a region. In tropical West Africa, root crops such as yellow guinea yam (*Dioscorea cayenensis*), white guinea yam (D. *rotundata*), kafir potato *(Plectranthus esculentus),* yam pea (*Sphenostylis stenocarpa*), and piasa (*Solenostemon rotundifolias*) dominate intercropped gardens. In semi-arid and arid areas of Africa, pearl millet (*Pennisetum glaucum* (L.) R. Br.) and sorghum (*Sorghum bicolor*) are intercropped with cowpea (*Vigna unguiculata* (L.) Walp.).

In many areas of the world, intercropping still dominates the cropping systems. This is particularly true of specific plant species. Okigbo and Greenland (1976) estimate that 80% of the cultivated area of semi-arid West Africa is intercropped. In Latin America, Francis (1978) estimated that 60% of the maize and 80% of the field beans are intercropped. In India, the majority of pigeonpea is intercropped. In tropical Asia and the Pacific, multi-storey intercropping is common with tree species that dominate the upper canopy. Currently there is renewed interest in strip-intercropping in developed countries. As our environmental and production concerns increase it is likely that intercropping will provide some profitable alternatives.

Measuring productivity in intercropping system

Yield comparisons

Early methodologies used to describe population dynamics were associated with animal ecology (Lotka 1925; Volterra 1928). From these works came the Lotka-Volterra differential equations that express population changes over time in terms of the inhibitory effects of competing populations and environmental limits. De Wit (1960) successfully applied these equations to interacting plant communities. By 1965, De Wit and van den Bergh characterized the performance of different species in a replacement series design by using the relative yield total (RYT) concept. The RYT is the sum of the relative yields (total biomass) of the species in the mixture and is expressed as the ratio of the yield of a species in the mixture to its yield in monoculture:

$$RYT = r_a + r_b + \text{----} + r_n$$

where r_a and r_b are the relative yields of species a and b, respectively, computed as the ratio between intercropped and sole crop yields. Values greater than one indicate that the two species are at least partially complementary, whereas values less than one indicate that the two species are competitive and, thus yield more when grown separately. This approach is not suitable for describing how the yield will behave in a mixture in which plant density is not constant (Inouye and Schaffer 1981).

Agronomic research methodologies that could provide useful evaluations of differences between sole and intercropping plantings were developed between 1970 and 1980. Most notable was the proposal and eventual widespread use of the land equivalent ratio (LER) (Willey and Osiru 1972; Willey 1979; Beets 1982; Spitters and van den Bergh 1982). A number of reviews of these works have been presented (Francis 1986; Ofori and Stern 1987; Francis et al. 1976; Fukai 1993). These summaries have been supplemented by a number of international workshops. Common to all these approaches is the use of replacement series plot designs where intercropping mixtures (two crops) are compared with sole plantings of each crop. The systematic requirement of this approach often results in crop mixtures not found in farmers' fields. Another major problem in using the LER in additive experiments is the effect of total plant density that occurs when a high density of one crop is combined with a low density of the other, i.e., the proportional composition and density of the mixture and their effects cannot be determined (Harper 1977; Trenbath 1976; Spitters 1980). Such problems have been addressed by standardizing sole crop populations (Willey and Osiru 1972; Mead and Willey 1980). Snaydon (1991) argues that LER values consistently underestimate complementarity because plant densities are held constant. This conclusion was reached by comparing the results from a number of replacement and additive experiments. Ultimately the derivation of LER values reflects the experimenter's objectives in comparing intercropping with sole cultures, whether or not these are the objectives of the farmers.

Using relationships described by his predecessors (de Wit 1960; Willey and Heath

1969), Spitters (1983) developed a method of estimating the degree of intra- and inter-specific competition from the total biomass yield of species in a mixture. This approach differed from earlier attempts in that two independent expressions are used that estimate the competition effects in situations where the species in a mixture are complementary in resource use and the condition of fixed density is not met. This work was carried farther by Ranganathan (1992), who introduced an economic component to these expressions. Calculation of economic returns provides an alternative measure of potentials for various intercropping combinations.

These later studies provide us with an acceptably robust means of describing intra- and inter-specific competition in various intercropping combinations. Use of a specific index is often driven by researcher objectives. Such indicies can give the necessary qualifications to relate to farmers' conditions but will remain open for criticism on their ability to relate to real conditions or express desired changes or outcomes in existing intercropping systems.

Sunlight comparisons

Measurements that indicate overall yield advantages or disadvantages of intercropping tell us little about which environmental resources are limiting and how competition is affected by different planting arrangements. Measurements of resource utilization in different intercropping systems have been carried out at a number of locations and with a wide range of plant species. Understanding how resource utilization is affected by changes in planting patterns allows researchers to predict changes in crop management and implement strategies that will result in more efficient resource use.

Total system light interception is determined by crop geometry and foliage architecture (Trenbath, 1983; Tsay, 1985). Advantages individual species might have in a mixture can be temporal and spatial. A slow-growing crop might not be affected by a faster growing species because the faster growing species might be harvested before the slower-growing one competes for sunlight. Successful intercropping combinations are oftentimes those that capitalize on both spatial and temporal complimentarity, thus resulting in an overall increase in light intercepted by the system during a season.

Two factors that affect yield in relation to incident radiation in an intercropping system are the total amount of light intercepted and the efficiency with which intercepted light is converted to dry matter (Keating and Carberry 1993). There have been studies in which sufficient measurements have been taken to derive such estimates. Willey et al. (1983) measured leaf area duration (LAD) in a sorghum (*Sorghum bicolor*)/pigeonpea (*Cajanis cajan*) intercropping system. Sorghum dry matter production in this study was only 5% lower than sole crop yields, whereas pigeonpea dry matter production was 53% of a sole crop. In this system, the faster growing crop (sorghum) was planted at a density close to that of the sole crop and received little competition from the slower growing species (pigeonpea) early in the season. Similar results have been obtained from intercropping mixtures of two slow-growing understory species that have shorter maturity times than pigeonpea i.e., pigeonpea/soybean and pigeonpea/groundnut.

Efficient light distribution through a canopy is a strategy found in intercropping

systems that achieve greater light energy capture. This approach is most common in tropical areas where the upper canopy is a tree species. In such systems, light levels below the tree canopy are relatively constant but lower, thus plant spacings in the understory can be adjusted to make full use of available light. Whereas this same approach may contribute to over-yielding in annual intercropping systems, it is more difficult to quantify or manage. Studies that have compared genotypes of different heights in intercropping reported no significant advantages (Pendleton et al. 1963 - maize; Osiru 1974 - sorghum).

Many of the perceived advantages in managing light in intercropping are based on the ability to use a faster growing species (C_4) at the top of the canopy and a slower growing species (C_3) at the bottom of the canopy. To a large extent this represents what is found in natural plant communities and many traditional intercropping systems. Such advantages in intercropping will be best utilized if two species used do not compete for sunlight at the same time. For intercropping combinations like soybean/pigeonpea and groundnut/pigeonpea, the issue of light is less important because each species has a significantly different growth curve (Ranganathan 1992).

As we strive to improve our understanding of resource use in intercropping systems it is quite likely that modeling of different factors will become a more powerful tool. A number of models have been developed that simulate canopy development (Saeki 1960; de Wit 1965; Duncan et al. 1967; Trenbath 1972). Through validation and further development, these models hold great potential in helping us develop a better understanding of light use in intercropping systems and a better basis for developing improved intercropping systems (Keating and Carberry, 1993).

Water use comparisons

For the arid and semi-arid areas of the world, water use is of great importance in determining resource utilization in intercropping systems. Problems abound in selecting research methodologies that will allow partioning of intercrop competition components. Because of these problems, many studies that have reported increased water use efficiency (WUE) in intercropping systems arrived at their conclusions through indirect measurements. Snaydon and Harris (1979) and Baker and Norman (1975) feel that below-ground competition and, more specifically, competition for water may result in intercropping advantages and disadvantages.

Species differences in rooting depth, lateral root-spread and root densities are factors responsible for water use competition and complementation (Babolola 1980; Haynes 1980). Although we have little direct knowledge of these factors and their interactions in intercropping systems, complementarity in water use has been cited as an advantage in intercropping (Natarajan and Willey 1980; Reddy and Willey 1981).

Plant species react differently to water stress conditions, thus it is unlikely that intercropping mixtures of cereal and legume species will compete uniformly when water becomes a limiting factor. Species that have higher water use or extraction will become stronger competitors. This is illustrated by a maize-cowpea study (Hulugalle and Lal 1986) in which WUE was higher in the intercrop when water was not a limiting factor, but under drought stress conditions WUE decreased rapidly in the intercrop and sole cowpea

plantings but increased in the sole maize planting. Morris and Garrity (1993b) report no significant differences in total water uptake between intercrops and sole crops, but WUE by intercrops ranged from 18% to 99% greater than in sole crops. Mechanisms they propose as being responsible for increased WUE include: (a) capture of a larger portion of evapotranspiration (ET) as transpiration by intercrops; (b) interception of more light by intercrops; (c) greater efficiency in dominant species components; (d) higher transpiration efficiency by crop mixtures; and (e) reduced boundary layers in the "rough" canopy of intercropping patterns (compared with uniform canopies of monoculture).

Nutrient use comparisons

Nutrient use in intercropping systems has received considerable attention despite difficulties in quantifying beneficial or competitive effects. Increased nutrient uptake in intercropping systems can occur spatially and temporally (Morris and Garrity 1993a). Differences among species in nutrient uptake and among various nutrients in their uptake mechanisms make the measurement of competition effects difficult. Soluble ions, such as nitrate, move freely in the soil solution and may travel up to 1.5 cm to roots (Barber 1962; Trenbath 1976). Nutrients not found in high concentrations in the soil solution but held on the clay surfaces (calcium, phosphorus, potassium) move to plant roots primarily by diffusion. These nutrients move only short distances, thus increasing their uptake is more related to increased root mass. Temporal advantages in nutrient uptake occur when crops in an intercropping system have peak nutrient demands at different times (Willey 1979).

Of the major nutrients, nitrogen (N) has received the most attention. This is both because N is most often limiting in areas where intercropping is practiced, and because combinations of legumes and non-legumes most often dominate intercropping systems (Ofori and Stern 1987). In these combinations, popular wisdom says that the key role of the legume component is its contribution to the N-economy of the system. Though often stated, this remains a point of debate (Fujita et al. 1992). Tree intercropping, a common system in tropical regions, gains substantial nutrient input from decomposed litter (Sanchez et al. 1985).

To what extent legumes contribute to the N-economy of intercropping systems is not fully understood. There is evidence that legumes capable of fixing atmospheric N_2 will reduce competition for N from the cereal component (Trenbath 1967; Fujita et al. 1992). Thus the absence of an N-fixing system will result in both crops competing for the same N-source, particularly when soil-N levels are low (Chang and Shibles 1985; Ofori and Stern 1986).

Fujita et al. (1992) present an excellent review on the role of N-fixation in mixed legume-cereal systems. N_2-fixation is much better understood than N-transfer to non-legumes (Stern 1993). Legumes appear to contribute to the N-economy of intercropping systems by transferring N to the cereal crop during the growing period (Ofori and Stern 1987; Rerkasem and Rerkasem 1988; van Kessel and Roskoski 1988; Eaglesham et al. 1981; Ofori et al 1987) or as residual-N that is available for the subsequent crop (Papastylianou 1988; Nair et al 1979; De 1980). A number of mechanisms have been reported that affect N-transfer (Ta et al. 1986; Ofosu-Budu et al. 1990; Fujita et al. 1990; Brophy and Heichel 1989;

Hawes and Lin 1990). Despite numerous studies on this subject, N transfer mechanisms and what factors affect the functioning of these mechanisms are still poorly understood.

The amount of N available either during or following an intercrop containing legumes will depend on conditions that impact legume N-fixation. A number of studies have shown that indeterminant legume types fix more N than determinant types (Francis 1986; Graham and Ross 1978). These findings appear to be species dependent and are not supported by studies in which different species were used (Ofori et al. 1987; Ogata et al. 1986). These studies suggest strong species and genotype differences that have not been fully documented.

Native soil-N levels and the amount of sunlight reaching legume species will affect N_2 fixation. Nearly all legumes fix less atmospheric-N if the soil has a high N-content, through either high native fertility or the application of fertilizers to the intercropping mixtures. These factors support traditional strategies used by farmers who select indeterminant, climbing legume species that are intercropped in systems with little or no additional fertilizer input. In these systems, although legume benefits will be maximized, production levels may be unacceptably low.

Gross residual benefits from intercropping systems containing legumes are less difficult to measure, and thus have received more attention. These benefits are measured as the amount of additional N required in a subsequent crop to achieve a similar yield as a crop that does not follow an intercrop containing a legume component. Although such estimates are quite variable and depend on agro-enviromental conditions, they provide a general idea of expected benefits from legumes. Apart from yield increases there are reported beneficial soil effects attributed to legumes in intercropping systems (Phetchawee et al. 1986; Normal et al. 1990). These advantages appear substantial; however, there is concern that the nutrient benefits from legumes in intercropping are limited to low-input systems (Heichel 1987). To address this question it will be necessary to choose legumes for intercropping systems that will fix nitrogen at soil-N levels capable of supporting acceptable cereal yields.

Rooting patterns

Below-ground competition or complementarity is a possible reason for under- or over-yielding in intercropping systems. Although such interactions are likely to be important, studies that have effectively measured below-ground competition in intercropping systems are difficult to find. The argument exists that intercropping systems have an advantage over sole cropping systems because of spatial differences in root mass that allow the combination to explore a greater root volume.

The difficulty in obtaining accurate measurements of root interactions in intercropping has been a major impediment in advancing our knowledge in this field. Despite this, a number of researchers have documented root interactions (Assemat et al. 1981; Willey & Reddy 1981; Regnier et al. 1989; and Perera et al. 1992). Their results were obtained by using root partitions and giving data on no-competition, shoot-competition only, and full-competition. Other studies have used defoliation to partition root interactions (Jeangros & Nosberger 1990; Seager et al. 1992). However, results from these studies can be criticized

because defoliation also reduces root competition in some species (Remison & Snaydon 1980).

Snaydon (1991) argues that below-ground competition is most often responsible for competition in intercropping stands. This argument is based largely on additive mixtures where relative yield total (RYT) values are compared. He also points out that in tropical and sub-tropical areas where intercropping is most frequently practiced, soil nutrients and water most often limit plant growth. We suspect that more attention has been given to solar radiation because it is easier to measure than the root-soil complex of interactions and function.

More than any other environment shared by intercrops, the underground portionis is the least understood. Accurate, direct measurements of root complementarity and competition are difficult. Continued use of indirect measurements will not provide complete answers. Recently introduced methods, such as the use of mini-rhizotrons and micro-sensors used to determine plant rhizophere conditions, will greatly assist us in obtaining the direct measurements necessary to better understand below-ground interactions in intercrops. These developments will be enhanced by further model development, resulting in a fuller understanding of the mechanisms and interactions responsible for beneficial effects measured in intercropping combinations.

Pests and diseases in intercropping systems

A large body of literature exists on how specific insects are affected by crop mixtures (Litsinger and Moody 1976; Perrin and Phillips 1978; Altieri and Schmidt 1986; Risch et al. 1983). With the interest in integrated pest management (IPM) it is highly likely that intercropping in its current forms will provide a logical base for future IPM programs.

Central to IPM issues are changes in pathogen populations as a result of diversification in a cropping system (Eguinjobi 1984). Hasse and Litsinger (1981) have summarized the effects of intercropping on insect pest populations. They have listed camouflage, crop background, masking or dilution of attractant stimuli, and repellent chemical stimuli as factors that interfere with insect host-seeking behavior. Factors such as mechanical barriers, lack of arrestant stimuli, microclimatic influences and biotic influences can interfere with insect population development and survival. It is likely that in many intercropping systems more than one of these factors is operational (Tahvanainen and Root 1972).

Specific references to each of those factors are presented by Hasse and Litsinger (1981). Since that time many research reports have been published on the effects of different intercropping systems on insect populations. Much of this work has been aimed at understanding insect population dynamics as they might relate to developing and implementing IPM programs. In some cases, reported results contradict each other. In India, *Helicoverpa armigera* populations were higher in sorghum/pigeonpea intercropping systems than on sole pigeonpea plots, and these higher numbers led to higher grain losses in the sole crops (Bhatnagar and Davies 1981). Later findings on the same intercropping system (Duffield 1993) indicated that egg parasitism in *H. armigera* by *Trichogramma spp.* (*Hymenoptera: Trichogrammatidae*) in sorghum resulted in low damage levels in sorghum but

that there was little transfer of this parasite to pigeonpea plants, relulting in severe yield losses in pigeonpea from *H. armigera.* These results suggest a potential IPM strategy of synchronizing the timing of flowering of both species so that maximum parasite transfer to pigeonpea can take place. It has been observed that chemical control of *H. armigera* in medium-duration sole pigeonpea plots is difficult, whereas control in intercropping plots is considerably easier once the sorghum has been removed. This difference is attributed to a better spray coverage because of increased distances between pigeonpea rows once the sorghum has been removed.

A study of intercropping pigeonpea and cotton found that LER advantages in the intercropping system were the result of improved insect control in the intercropping treatments and not complementarity between the two plant species (Potdar et al. 1994). Because this intercropping system is commonly used in parts of India and because there is no clear evidence of complementarity between the plant species, it is thought that the popularity of this system rests on its advantages in controlling *Heliocoverpa armigera,* a major pest of both species in the mixture. In a study that compared *Heliothis* damage in cotton intercropped with corn, soybeans, alfalfa, peanuts, and sorghum, Robinson et al. (1972) found that insect damage in cotton was less when it was intercropped with sorghum. In the same study, they found that the frequency of *Heliothis* predators was higher for sorghum.

In many intercropping studies, plants are protected against insect attack, a practice not often found in practical on-farm intercropping settings. This raises the question of how appropriate are the improved genotypes that are bred and screened in protected environments to intercropping settings managed at low input levels. Ehlers (1994) reports that the yields of cowpea genotypes tested under protected conditions were similar in sole and intercropped plots, whereas the intercrop plots yielded less in unprotected conditions. Ehlers suggested that identifying genotypes under protected conditions will not result in the selection of genotypes well suited for conditions generally found in farmers' fields. Current ongoing work at ICRISAT has shown that sorghum genotypes that perform better than farmers' varieties under protected, irrigated, and well fertilized conditions, will not necessarily perform better in farmers conditions. This work has identified the pest shoot fly as a major constraint that is highly interactive with fertility and genotype.

Fewer studies have been done on the effects of intercropping on plant diseases than those on insect pests (Francis 1986). There is evidence that intercropping reduces disease incidence in some crops when compared with sole crops (Larios and Moreno 1977; Palti 1981; Thresh 1982). In some cases, recorded advantages of disease control through intercropping were the result of reduced insect vector numbers; thus disease control was more a function of improved insect control. Natarajan et al. (1984) reported that intercropping sorghum and pigeonpea reduced fusarium wilt incidence in pigeonpea when compared with sole plantings. In these studies, pigeonpea yields were greater than partial expected yields, but no higher than sole crop yields. The reduction of fusarium wilt was consistent across 14 susceptible genotypes. Similar results did not occur when maize was used as the intercrop. These studies suggest a potential of managing disease problems through intercropping, however, more information is needed before intercropping systems can be designed to capitalize on disease control mechanisms.

The role of intercropping in controlling pests and diseases is likely to receive much attention as we become more concerned with pesticide use and environmental issues. It is quite possible that much of the renewed interest in intercropping will evolve around issues of pest and disease control. To date our understanding of crop/insect interactions in intercropping is incomplete, and the effectiveness of this type of protection is unpredictable (Trenbath 1993). Given the resilience of traditional systems it is evident we still have much more to learn.

Social and economic implications in intercropping systems

The mere fact that intercropping systems have maintained their importance through significant economic and structural changes in world agriculture is testimony to their resilience. Regardless of what levels we reach in understanding the physical and biological processes of intercropping systems, it is ultimately the farmers who make the choice to keep, modify, or discard any particular system. It is also the farmer who selects what plant species will be intercropped and how each mixture will be managed. It is difficult for physical and biological scientists to understand the social and economic forces that determine whether farmers' maintain or improve intercropping systems and to realize that it is these same forces that have made intercropping systems so difficult to change.

The most often stated reason for intercropping is risk reduction. This theory is supported by the fact that as agriculture moves to a better environment, intercropping becomes more prevalent (Norman 1974; Abalu 1976). This may be the case even if overall income is reduced (Sanders and Johnson 1982). Furthermore, Jodha (1977) reported that intercropping is more extensively practiced by small farmers. Risk, as it applies to subsistence farmers, relates more to net production and less to market forces. The fact that subsistence and commercial farmers exist in areas where intercropping is practiced suggests that we must consider prices or economic buffering in any evaluation made of intercropping systems. This is problematic in that prices on input and produce are variable over both time and space. These variations could offset or enhance any production gains from intercropping. Using risk as a criterion for evaluating stability of intercropping systems, Mead et al. (1984) showed that the probability of reaching a given income level was higher in an intercrop when compared with sole crops of the same component species. Such analyses are valuable when evaluating probabilities of success for experimental data and for predicting possible adoption of given management changes to intercropping systems. However, the analyses suffer from not being able to represent either the complexities of intercropping systems or the socio-economic conditions under which the farmers operate.

Future research needs

When we consider the future needs of intercropping research, it is important that we should not engage in "agronomic trivial pursuit" (Youngquist and Francis 1988), There

have been sufficient studies indicating advantages in total dry matter production or grain yields in intercropping systems. To repeat this same research and not obtain data that will help us identify the mechanisms responsible for intercrop differences would indeed be a trivial pursuit. Given recent advances in data collection and modeling, it is time to move forward with better quantification of "why" intercropping is advantageous in many situations. Much of the current and future interest in intercropping will come from people with environmental concerns and from those who measure both total production and economic consequences of intercropping. We can build on this growing interest to better understand topics such as below-ground competition, nutrient management, system design, and applications of specific systems by farmers in each unique ecological and economic situation.

Lastly, but most important, we must strive to better understand why intercropping has remained such an important part of agriculture systems in many parts of the world. Through this understanding we may make useful recommendations to farmers on how they can improve current systems and not on how to eliminate well-established, sustainable systems. This implies that research must come much closer to addressing farmers' needs and should respect farmers' goals. In the field of genetic improvement it would be advisable to test new genotypes before they are released for their performance in intercropping systems, particularly when they are targeted to intercropping systems. The management of intercropping systems is complex and management changes will need to be carefully considered. Okali et al. (1994) point out that in 20 years of experience in Niger it is evident that agricultural extension programs based on technical recommendations that essentially restrict the farmers' choice will have little if any positive impact. What does that tell us about our research efforts?

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Significance of Legumes in Intercropping Systems

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Abstract

Cereal/legume intercropping generally increases dry matter production and grain yield more than their respective monocultures. The efficiency of production depends on several factors including the population density of component crops, soil-nitrogen (N) status, and genotype of component crops, especially legume. The dry matter contribution of component cereal is important to ensure greater efficiency.

Biological nitrogen fixation (BNF) plays an important role in the N economy of cereal/legume intercropping systems. For instance, BNF accounted for between 75 and 78% of the total N accumulated in soybean, and N-transfer between 11 and 58% of N accumulated in component sorghum. Nitrogen-transfer increases the cropping system's yield and efficiency of N use. The closeness of root systems of component crops is important to ensure N-transfer.

Although currently fixed-N compounds, such as ureide, are released from roots of ureide producing legumes, BNF and N-release are not directly related. The release of N compounds might be related to the energy metabolism of roots and nodules. It is suggested that factors that will result in low root adenosine triphosphate (ATP) production may promote N-release. Low ATP levels may affect the root membrane permeability.

Mutual shading by component crops, especially the taller cereals, reduces BNF and yield of the component legume. Light interception by the legume can be improved by selecting a suitable plant type and architecture. Planting pattern and population at which maximum yield is achieved also vary among component species and environments. Crops can be mixed in different proportions from additive to replacement or substitution mixtures. At an ideal population ratio, a semi-additive mixture may produce higher gross returns.

Beneficial effects of mono- and intercropped legumes on subsequent cereal crops have been demonstrated in terms of increase in biomass production, which is mainly due to increase in soil organic matter, improved soil structure, etc. The benefits of intercropping in subsequent crop production is almost equivalent to that of well-fertilized crop in some cases. The N availability from residue of previous crop varies depending upon either cereals or legumes and legume variety.

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Introduction

Intercropping is an age-old, widespread practice in the warmer climates of the world (Agboola and Fayemi 1972; Searle et al. 1981), especially the tropics (Willey 1979). The method allows maximum utilization of natural resources available for production. Total grain and plant N-yields can often be increased by intercropping legumes with non-legumes (Singh et al. 1986). Most farmers in developing countries have adopted this low-input system principally for climatic and socio-economic reasons (Okigbo and Greenland 1976). Growing interest in intercropping in developed countries (Ofori and Stern 1987) stems from an increasing awareness of environmental degradation arising from high chemical inputs (Nielson and Mackenzie 1977) and gives rise to a search for ways to reduce modern agriculture's overdependence on fertilizers, manufactured mainly with the use of fossil energy.

Crop varieties grown vary by region, depending on several factors including rainfall, and edaphic and socio-economic factors. Crop mixtures may be legume/legume (Rao and Mittra 1989) or legume/non-legume (Mandal et al. 1990).

Biological nitrogen fixation (BNF), which enables legumes to depend on atmospheric nitrogen (N), is important in legume-based cropping systems when fertilizer-N is limited. BNF contributes N for legume growth and grain production under different environmental and soil conditions. In addition, the soil may be replenished with N through decomposition of legume residues. Evidence also suggests that associated non-legumes may benefit through N-transfer from legumes (Fujita et al. 1990).

Yield advantages from intercropping as compared to sole cropping are often attributed to mutual complementary effects of component crops, such as better total use of available resources like soil-N and moisture, and BNF. Generally, monocropped legumes have higher yields than in intercropping systems. However, in most cases when little or no N-fertilizer is applied, land productivity measured by the Land Equivalent Ratio (LER) and monetary gain clearly show the advantages of intercropping of cereals and legumes (Mandal et al. 1990; Yunusa 1989). In some cases, however, no benefits of intercropping have been reported (Cenpukdee and Fakai 1992a). This discrepancy may be due to interspecific differences in plant architecture, absorption efficiency of nutrient and soil moisture, and BNF, and so on.

Several researchers have studied the advantages of intercropping of cereals and legumes (Agboola and Fayemi 1972; Ofori and Stern 1987). Willey (1979) and Francis (1989) have provided insight into the biological interactions of intercropping systems in general, whereas Ofori and Stern (1987) dealt with cereal/legume intercropping systems in particular. More recently, a number of papers have been published on dinitrogen (N_2)-fixation and N-release and, more importantly, the need to develop legume-based technologies to sustain agricultural production.

In the present paper, significance of legumes in intercropping, particularly transfer of N from legume to non-legume, will be emphasized, and recent information and its implications with respect to optimum use of BNF and solar radiation will be reviewed. The physiological relationship between N_2-fixation and N-release and the N economy of the total system are considered.

Common intercropping systems

Growing legumes and cereals together for food production is not only popular among subsistence farmers in the tropics, who produce the bulk of food in developing countries, but is also expanding to warmer regions in the subtropics. Intercropping is practiced under different climatic regions such as the humid tropics (Agboola and Fayemi 1972); semi-arid regions (Faris et al. 1983), Mediterranean regions (Ofori and Stern 1986), and in temperate climates (Fujita et al. 1990). The system's benefits are realized in areas where the rainy season is long and favorable enough to grow more than one crop of different duration simultaneously or successively (Okigbo and Greenland 1976), or where irrigation is available (Mandal et al. 1990). Some reports indicate benefits even for dry and unpredictable rainfall conditions (Papastylianou 1990).

Legumes are a major component in cropping systems of developing countries. In the Latin American tropics, between 80 and 90% of beans are produced in intercropping systems (Francis et al. 1976). In the Indian subcontinent, pigeonpea is in almost every cropping system (Patra and Chatterjee 1986). Amount and distribution of rainfall, soil fertility, socio-economic, and other cultural factors influence the composition of the component crops. In low and unpredictable rainfall areas where irrigation is unavailable, early maturing and/or drought resistant legumes and small-grained cereals are cultivated. Examples are finger millet and green gram in India (Kaushik and Gautam 1987), oats and vetch in Cyprus (Droushiotis, 1989), cowpea and sorghum in the sub-Saharan West African sub-region (Ntare 1989). In seasons or areas where rainfall is abundant, maize and rice are often planted with such legumes as field bean, cowpea, and soybean (Ezumah et al., 1987).

The first of the two main methods of intercropping cereals and legumes is superimposition of one crop on another as described for maize/beans (Fischer 1977) where the total plant population per unit area is higher than the optimum population in monoculture. The second is a replacement type, where various proportions of one component crop replace the same proportions of the other component crop in the mixture (Yunusa 1989). The second system is receiving increased attention of scientists because of reduced intercrop competition and increased total yield.

Benefit of intercropping for biomass production

Greater amount of biomass, seeds, and N yields in intercropped legumes and non -legumes compared to their respective monocrops has been reported (Rerkasem and Rerkasem 1988 ; van Kessel and Roskoski 1988 ; Fujita et al. 1990). The higher biomass production is frequently due to the enhanced growth of the component non-legume. Because the non-legume is generally taller than the legume and can therefore intercept adequate solar radiation, biomass production of the non-legume is more closely related to improved N nutrition (Rerkasem and Rerkasem 1988; Fujita et al. 1990; Ofosu-Budu et al. 1993a).

In sorghum/soybean intercropping, whole plant weight of sorghum significantly correlated with its N content irrespective of population density (Fujita et al. 1990). At higher population densities, intercropped sorghum had a higher N content than

monocropped sorghum. A close relationship between the whole plant weight and N accumulation has also been observed in sorghum but not in soybean under conditions where soil-N content is extremely low and capacity to supply N from soil is limited (Ofosu-Budu et al 1993a). A number of studies showed that the N-use efficiency for dry matter production differs between legume and non-legume. For instance, Shinano et al. (1991) compared biomass production and N absorption among five major crops in Hokkaido, Japan, and found that soybean had a lower N-use efficiency than cereal crops, such as maize, spring wheat, and rice.

This evidence indicates that in legume/non-legume intercropping, increasing N content of the non-legume is a key factor in enhancing biomass production and N-use efficiency.

Nitrogen balances in legume-cereal intercropping systems

The main N sources in cereal/legume systems are N fixed through BNF by the legume component, fertilizer-N, and soil-N. The only published data illustrating N budgeting are on studies conducted with maize and cowpea by Eaglesham et al.(1981) in Western Nigeria and Ofori et al. (1987) in Western Australia. Using the equation suggested by Rennie et al. (1982) to calculate N from fixation, fertilizer, and soil, Eaglesham et al. (1981) prepared a N-balance sheet for the system. The N contribution by seeds of maize and cowpea at sowing was less than 2 kg ha^{-1}, fixed-N by component cowpea was about 41 kg ha^{-1}, N from fertilizer was 3 kg ha^{-1}, and soil-N was 53 kg ha^{-1} with total N in the crop at about 99 kg ha^{-1}. Assuming a seed-N harvest index of 36% for cowpea and 90% for maize, the quantity of N removed in the intercrop system was about 52 kg ha^{-1} (28 kg ha^{-1} from maize and 24 kg ha^{-1} from cowpea) leaving about 46 kg ha^{-1} in the residues.

The resulting net changes in soil-N after grain harvest and the return of residues are calculated as N = N (residues) - N (uptake from soil). The maize-cowpea intercrop would result in a loss of 14 kg N ha^{-1} to the soil, compared to a 21 kg N ha^{-1} loss after sole cropping of maize and a 36 kg N ha^{-1} gain after sole cowpea.

The data of Eaglesham et al. (1981) indicated that, compared with cowpea monocropping, intercropping maize and cowpea does not excessively deplete soil-N. Cowpea monocropping might enhance soil-N status and could benefit a subsequent cereal in a legume/cereal crop rotation, provided the high N content stover is returned to the soil. In contrast, sole cropping maize depletes the soil-N. Similar observations were reported by Ofori et al. (1987).

BNF in legume-cereal mixed cropping systems

The amount of N fixed by the legume component in legume-cereal intercropping systems depends on several factors, such as species, plant morphology, density of component crops, type of management, and competitive abilities of the component crops (Ofori and Stern 1987). Variation in BNF activity among legumes has been reported with both mono- and

intercropping systems.

Effect of plant type

Indeterminate legumes fix more N than determinate types in intercropping. Graham and Rosas (1978) and Francis (1986) observed that BNF in climbing bean was unaffected by intercropping with maize. However, BNF estimated by the acetylene reduction activity (ARA) of a determinate soybean type decreased when intercropped with sorghum (Fujita et al. 1990). A similar phenomenon was observed in intercropped siratro, a climbing legume (Ogata et al. 1986), and cowpea (Ofori et al. 1987; van Kessel and Roskoski 1988). Higher BNF activity of ricebean in an intercrop than in a monocrop was mainly due to its vigorous climbing habit which allows increased interception of solar radiation. The contribution of N_2 fixation to ricebean N yield was greater in intercrops than in monocrops even at the lowest maize-ricebean ratio (Rerkasem et al. 1988).

Combined N effect

With no applied N, shading did not affect N_2-fixation by the component groundnut crop, although incoming light reaching the legume was reduced by 33% (Nambiar et al. 1983). When 50 kg N ha^{-1} was applied, BNF was reduced by 55%, although light reaching the groundnut was 54% of incoming radiation. This suggests that heavy application of combined-N significantly reduces BNF.

The role of soil-N (organic matter) in the N nutrition of a sorghum/soybean intercropping system has recently been studied in soils differing in N content (Ofosu-Budu et al. 1993a) using the ^{15}N-dilution method. Evidence suggests that on soil with a relatively high N content (high organic matter) the intercropping yield increased by 25% due to enhanced soil-N uptake by the sorghum component, whereas the soybean component depended mostly on BNF. Dinitrogen fixation and N-transfer were about 35% higher in the high-N soil (4.2×10^{-4} kg N kg^{-1} soil) than in the low-N soil (1.3×10^{-4} kg N kg^{-1}soil).

Effect of light

Because N_2 fixation is energy-dependent, a reduction in the photosynthate supply to the nodules is detrimental. If the non-legume is taller than the legume, shading occurs and results in reduced photosynthesis and N_2-fixation (Wahua and Miller 1978). In fact, partial defoliation of component sorghum increased sunlight availability and increased the BNF of the intercropped groundnut (Nambiar et al. 1983). Total N fixed in a cowpea/maize system at different spacing was more dependent on the type of cropping system (generally lower in mixed than in monocrop cowpea) than on the crop spacing (Ofori and Stern 1987; van Kessel and Roskoski 1988).

Plant density has also been reported to influence N_2-fixation, but total N_2-fixation activity on an area basis appeared less variable. Using the ^{15}N-dilution method, van Kessel and Roskoski (1988) reported that the percentage of total N derived from N_2 fixation in cowpea was largely independent of spacing and, overall, cowpea derived from 30 to 50% of

its N from BNF. The reports indicate that plant density has little effect on quantity of N derived from dinitrogen fixation. More importantly, the BNF of the legume is not always reduced, but is dependent on the legume's ability to intercept light.

Interspecific differences in BNF response to shading have been observed. Fujita et al. (1993) reported that shading decreased the amount of fixed-N in centrosema, siratro, and kudzu, but the decrease in kudzu was less as found by no effect of 55% shading on its N-fixing activity. They assumed that the higher tolerance to shading in kudzu (*Pueraria lobata*) may be due to the utilization of the reserve root carbohydrate for BNF. These observations suggest that these may be genetic differences in tolerance to reduced light conditions and that such tolerance is a favorable characteristic of component legumes in intercropping.

Nitrogen transfer from legume to cereal

Symbiotically fixed-N has been considered a useful source of N to non-fixing plants (Virtanen et al. 1937) in intercropping systems. This N-transfer is considered to occur through root excretion, N leached from leaves, leaf fall, and animal excreta if present in the system. Evidence suggests that N_2 fixed by a legume component may be available to the associated cereal in the current growing season (Brophy and Heichel 1989; Eaglesham et al. 1981; Ta et al. 1989) or as residual N for a subsequent cereal crop (Searle et al. 1981; Singh 1983). Both current and residual-N transfer are important and could improve the N economy of legume-based intercropping systems. Other researchers have reported little or no current-N transfer in legume/cereal intercropping (Ofori and Stern 1987; Ofori et al. 1987; Rerkasem and Rerkasem 1988; van Kessel and Roskoski 1988; Danso et al. 1993). This suggests that N-transfer may occur only under certain conditions.

Danso et al. (1993) found that dry matter yield of oats was enhanced by 26% and N content by 21% by intercropping with a sweet-blue lupin. After critically examining the data from the isotope dilution and the total N-difference methods in their experiments and in earlier reports and their experiments, they suggested that the enhancement of dry matter yield and N content of intercropped oat could be attributed to an N-sparing effect and not to N-transfer.

Agboola and Fayemi (1972) found that 3% of the N fixed by green gram *(Vigna radiata* L.) was released into the root zone, and Eaglesham et al. (1981) showed that 24.9% of N fixed by cowpea was transferred to maize. Brophy and Heichel (1989) observed a release of 10.4% of symbiotically fixed-N in soybean (*Glycine max* (L.) Merr. cultivar Fiskeby). Release of about 30% of fixed-N by the soybean root system into the nutrient culture medium has been observed (Ofosu-Budu et al. 1990).

Nitrogenous compounds such as amino acids, proteins, and peptides were identified in leachates from root zones of legume seedlings grown under sterile sand conditions (Wacquant et al. 1989). Ofosu-Budu et al. (1990) found that about 10% of the N released was in ureide form in soybean. Ta et al. (1986) reported that recently fixed-N was the major source of N-release. However, Brophy and Heichel (1989) for soybean and Ofosu-Budu et al, (1990) for alfalfa found that soluble protein made up a larger portion of the excreted N. No direct relationship between ureide excretion and N_2-fixation was observed.

In general, the root zone immediately behind the root tip is considered the major site of exudation (Pearson and Parkinson 1961), but different sites have been reported for different plant species (Schroth and Snyder 1962). In soybean, Ofosu-Budu et al. (1990) found that the major N-release is from roots, with negligible release from nodules. Root caps of many plants, including legumes, shed cells that become part of a mucilaginous sheath around the growing root (Rougier 1981). These shed cells, products of root cap turnover, have traditionally been referred to as 'sloughed' root cap cells because it was believed they were dead (Paull and Jones 1976). However, reports suggest that the shed cells exhibit 90 to 100% viability, and in pea (*Pisum sativum* L.) on average 3,400 cells per root in water-culture conditions were observed (Hawes and Lin 1990). Assuming that these cells release their N content, the N-release by legumes to cereals could be substantial.

Factors affecting N-transfer

Nitrogen-release by legume root systems is not well understood, however it is controlled by both internal and external factors. Ofosu-Budu et al. (1993b) reported no direct relation between N-release and N_2-fixation. For example, super-nodulating soybean mutants, i.e., ntsl007 and nts1116, have a higher root-N content but a smaller N-release rate compared with their parent, soybean cultivar Bragg, suggesting the role of N-pool in roots on N-release is limited.

Fujita et al. (1990) found that out of three treatments that decreased BNF in soybean (pod removal, defoliation, and stem girdling), only stem girdling promoted N- release. Ofosu-Budu et al. (1995) found a similar pattern of N-release and ATP content in roots after shoot detachment and stem girdling and assumed that N-release from roots may be associated with energy status of roots through permeability of root membranes.

Benefits to associated cereals in intercropping systems have been suggested to be due to factors such as component crop densities, which determine the closeness of legume and non-legume crops (Fujita et al. 1990). In a soybean/sorghum intercropping system, N-transfer increased from 0.89 g N m^{-2} at 50 x 50 cm spacing to 2.05 g N m^{-2} at 12.5 x 12.5 cm spacing, and N-transfer estimated by the total N-difference method using sorghum as a non-N_2 fixing system was 5.6 and 20.1% of soybean N at the respective spacings.

Legume growth stages may influence the N-release rate. For unharvested alfalfa, the peak in ninhydrin-N release was near midgrowth cycle (Richter et al. 1968). Ofosu-Budu et al. (1990) also reported that N-release by the soybean root system was higher during the pod-filling stage. They attributed this to the relative increase in root size.

Although N-release mechanisms are unclear, some environmental factors appear to stimulate N loss from roots. A possible role of pectolytic enzymes in living root cell has been proposed (Hawes and Lin 1990). Furthermore, factors that promote N-release may be specific. High temperature (35°C) led to an increase in N released from soybean, sesbania, and Chinese milk vetch roots (Ofosu-Budu et al. 1992). However, lower temperatures (15 and 25°C) had no effect. Vancura and Stanek (1975) and Brophy and Heichel (1989) reported an increase in the release of various materials from roots after water stress. Possible reduction in transpiration resulting from water deficit and subsequent build-up of recently assimilated N in roots and nodules may result in passive loss of soluble-N. Water

stress is said to affect root cell membrane permeability (Hale et al. 1978). Iron (Whitney and Kaneshiro 1967) and phosphorus (P) stresses have been thought to promote N-release. It has also been suggested that release of some substances from the cereal component could stimulate N-release by legumes (Ta and Faris 1987; Wacquant et al. 1989).

Role of vesicular-arbuscular mycorrhizal (VAM) fungi on N-transfer

Nitrogen-transfer can be facilitated or enhanced by the presence of VAM fungi (Bethlenfalvay et al. 1991). It has been argued that VAM infection can provide channels for direct inter-plant N-transfer (Francis 1986). The endomycorrhizal fungus Glomus mosseae has been shown to translocate soil-^{15}N to mycorrhizal celery plants (Ames et al. 1983). When inoculated with VAM fungi, significant two-way nutrient transport between soybean and maize has been suggested (Bethlenfalvay and Ferrera-Cerrato 1990). This movement may be driven by a source-sink effect. When associated with nodulated soybean, P content in maize declined by 16% and N content increased by 22% (Bethlenfalvay et al. 1991). If such fluxes between plants are controlled by source-sink effects, high N concentrations in soybean could account for the N transported to maize, and high nodule P-requirement for the reverse flux of P. Interplant N-transport via hyphal connections would require a reversal of the normal direction of transport at the symbiotic interface in the donor plant, with efflux of N from the root cells to the apoplast and uptake by the fungus (Smith and Smith 1990). However, Hamel et al (1991a) reported that a reversal of N-transport between symbionts is biologically insignificant, even when senescence and death of the host have increased membrane permeability. They suggest that N-transfer between soybean and corn probably occurs indirectly, through N release into the soil followed by uptake that may be mycorrhizally assisted, rather than by direct transport between plants through VAM hyphae. Studying the hyphal transport of nutrients between plants is facilitated by a novel method of separating root compartments by a root-free zone and restricting root penetration by a fine mesh (Schuepp et al. 1987; Camel et al. 1991; Bethlenfalvay et al. 1991; Frey and Schuepp 1993).

Frey and Schuepp (1993) reported that transfer of ^{15}N from berseem (*Trifolium alexandrinum*) to the non-legume such as apple and maize infected by the VAM fungus was significantly higher than in the non-infected non-legume over a 28-day period, either when a split-root technique was employed to label the legume with ^{15}N or when the legume was labelled with ^{15}N by injection into the leaf petioles, 4.7 and 0.1% of the ^{15}N content of berseem was transferred to apple and maize, respectively.

Collectively, a number of studies demonstrate the possibility of N-transfer from legume to non-legume in intercropping systems under certain given conditions, such as infection of VAM fungi or direct contact of fine roots of each crops. However, the significance of N-transfer in N-balance in intercropping has not been quantitatively evaluated.

Most of the studies regarding mycorrhizal aided N-transfer were conducted in sterile soils. However, it was reported that mycorrhizal and soil microflora interact in many ways (Linderman 1988). Hamel et al. (1991b) observed that in spite of higher levels of root colonization and more abundant hyphae associated with plants growing in fumigated soil,

mycorrhizal-enhanced ^{15}N-transfer to maize was significant only in non-fumigated plots. They suggested that the effect of mycorrhizal fungi on soil microbial populations may be an important factor affecting N-transfer between mycorrhizal plants.

The occurrence of VAM fungi has been described in many agronomic crops (Kucey and Paul 1983). For example, Hicks and Loynachan (1987) reported the presence of VAM fungi in field-grown soybean. The VAM fungal genera (*Glomus, Gigaspora, Acaulospora,* and *Scutellospora*) were found to be associated with soybean rhizosphere soil in the district surveyed (Khalil et al. 1992). A reduction of VAM fungal root colonization in soils with added P-fertilizers is well documented (Bethlenfalvay et al. 1983; Hicks and Loynachan 1987). However, Khalil et al. (1992) reported that soybean roots from most soils, in spite of some soils having very high soil-test P levels, were extensively colonized (60-100%) by VAM fungi. This evidence suggests that N-transfer from legume to cereal in the intercropping system can be thought the effect of VAM fungi under natural soil conditions.

It has been shown that, when mycorrhizal donor plants were defoliated, the roots became senescent and the transfer of P to mycorrhizal receiver plants was greatly increased (Newman 1988). Similarly, it has been observed that N-transfer from forage legumes to grasses growing in mixture in the field, was stimulated by clipping (Ta and Faris 1987). Senescence could increase the permeability of the root cell membranes, and thereby provide a physiological basis for transfer from the host to the fungus (Smith and Smith 1990). Such phenomena could explain the rapid transfer of P from dying roots to the roots of living plants sharing mycorrhizal links (Newman and Eason 1989).

Decomposition of dead roots and nodules may be the dominant pathway for release of fixed-N from living legume plants. The first evidence for rapid senescence and decomposition of fine alfalfa roots was given by Jones (1943). He found that transient (noncambial) roots of alfalfa (*Medicago sativa* L.) lived only a few weeks. Dubach and Russelle (1992) found that 64% of fine alfalfa roots and 34% of fine birdfoot trefoil *(Lotus corniculatus* L.) roots at a 12 cm depth decomposed in the establishment year of the stand. Little nodule decomposition occurred over the first growing season in their experiment, Ta and Faris (1987) suggested that alfalfa may transfer fixed-N through root decay and birdfoot trefoil may transfer N through nodule decay. Dubach and Russelle (1994) reported that alfalfa releases more N through decomposing roots than nodules, whereas birdsfoot trefoil contributes more N to the soil through decomposing nodules than roots, but neither process could account fully for published estimates of N transfer.

Residual effects of 'legume/cereal' mixed cropping

Beneficial effects of mono-and intercropped legumes on subsequent cereal crops are well documented (Papastylianou 1988). For instance, wheat yield increased after a maize/soybean intercrop and a maize/cowpea intercrop (Nair et al. 1979), after a maize/groundnut or a maize/soybean intercrop (Searle et al. 1981), after a pearl millet/several legumes intercrop (Patil and Pal 1988). Barley yield also increased after oat (*Avena sativa* L.)/vetch (*Vicia sativa* L.) or peas (*Pisum sativa* L.) (Papastylianou 1990). Various factors, such as an increase in organic matter, improved soil structure, and, most

importantly, increase in soil-N, might account for this phenomenon.

The N uptake without fertilizer-N application by a subsequent wheat crop after cropping maize was 12 kg N ha^{-1}, after maize/soybean 19 kg N ha^{-1}, after maize/peanut 46 kg N ha^{-1}, and after peanut 54 kg N ha^{-1} (Searle et al. 1981). This shows that a subsequent crop could benefit as much from following maize/legume intercropping with no fertilizer-N applied as from planting after a sole-maize crop applied with 100 kg N. Singh (1983) estimated N benefits to wheat derived from various preceding legume intercrops. Comparing wheat after sole sorghum with wheat after intercrop, he obtained N fertilizer equivalents of 3 kg ha^{-1} with soybean, 31 kg ha^{-1} with green gram, 46 kg ha^{-1} each with grain cowpea and groundnut, and 54 kg ha^{-1} with fodder cowpea. Nitrogen uptake by a succeeding crop, when 100 kg ha^{-1} was applied to the preceding crop, was always higher following sole or intercropped cowpea. This could be due to less immobilization of the freshly applied fertilizer-N by legume crop residues rich in N (Patra et al. 1989).

Patil and Pal (1988) reported that 80 kg N ha^{-1} was saved for the succeeding bread wheat by the preceding pearl millet/black gram or cowpea intercrops. Nitrogen in crop residues can contribute a significant amount to the next crop and, compared with cereals, residues from legumes often contribute substantial amounts of N. Data on N availability from ^{15}N-labelled rice, soybean, and wheat to subsequent rice showed the minimum estimate of residue-N mineralized from the time of residue incorporation until harvest to be 9% of rice, 52% of soybean, and 33% of wheat (Norman et al. 1990). Residue-N recovered in the subsequent rice crop was 3% of the rice, 11% of the soybean, and 37% of the wheat residue. The higher the C/N ratio and the amount of N in the residue, the higher the amount of residue-N mineralized. Loss of easily decomposed N fractions of the soybean residue and the high N concentration of the wheat residue might explain why wheat residue contributed more N than soybean residue.

Improving productivity of legume based intercropping systems

Selection of component crops: Important characteristics of cereals and legumes

When grown in association, basic physiological and morphological differences between cereals and legumes affect their mutual relationship. Cereals are taller, have a larger mass of fine roots, and are adaptable to a wide range of environmental conditions, including low soil fertility. In intercropping, the component with its leaves higher in the canopy structure is at an advantage, particularly if the leaves are broad and horizontal (Trenbath 1976). Optimum conditions must be attained to realize good growth for legumes, especially if they will derive most of their N from BNF.

Soil N uptake by ricebean was markedly suppressed when intercropped, being 1.3 g N m^{-2} in intercropping against 6.4 g N m^{-2} in monoculture (Rerkasem et al. 1998). When monocropped at the same row spacing, both cowpea and maize took up equal amounts of soil and fertilizer-N (van Kessel and Roskoski 1988). The uptake of fertilizer- N is dependent on cropping system and row spacing. Highest N-uptake occurred in those

cropping systems with the highest plant population. No significant differences were found between monocropped maize and cowpea and the sum of intercropped maize/cowpea at the same row spacing. Component maize at the wider row spacing took up more fertilizer-N than maize at the narrowest spacing. Soil-N uptake was also a function of row spacing rather than of crop combination (van Kessel and Roskoski 1988). Patra et al. (1989) examined effects of intercropping on N-use efficiency in India. They reported that applications of 100 kg N ha^{-1} as urea was used more efficiently by intercropped maize/cowpea than by monocropped maize.

The rate of the crop dry matter production depends mainly on efficiency of photosynthetically active radiation (PAR) (Biscoe and Gallagher 1977). The mount of radiation intercepted by the component crop in an intercrop system depends on the geometry of the crop and foliage architecture (Tsay 1985). Generally the taller cereals shade the legume and cause reduced growth and yield of the legume at high densities. Component crops increase in height in intercropping systems, probably as a result of competing for light. Differential increase in plant height of component crops as a result of intercropping increases with increasing density (Fujita et al. 1990). The magnitude of the increase (plastic response) was more pronounced in sorghum than in soybean, suggesting that sorghum is better equipped to compete for light by elongating the stem and developing higher-positioned leaves (Fig. 1). When considering competition for light, this plant characteristic may be important in determining optimum plant densities for various cereal/legume systems.

Yield change in a maize-cowpea intercropping system in response to fertilizer-N

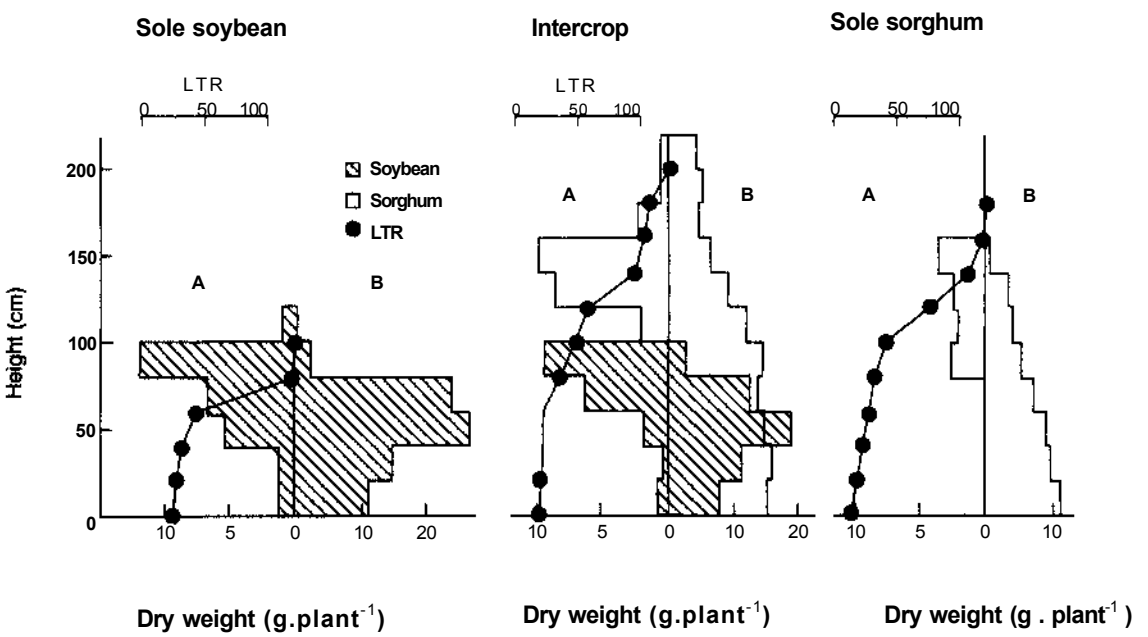

Fig. 1. Canopy profiles of plant dry weight and light transmission ratio at 17.7 (cm) x 17.7 (cm) spacing in mono- and inter-cropping of soybean and sorghum at 116 days after planting. A, leaf blade; B, stem + petioles (leaf sheath) + reproductive parts; LTR, light transmission ratio.

application was a reflection of the maize and cowpea architecture and growth habits (Ezumah et al. 1987). Maize grain yields increased 62% with N rates from 0 to 120 kg N ha^{-1}, while average cowpea yield decreased by 27%. The early maturing, determinate, semi-erect TVX 3236 cowpea cultivar did not respond to applied N, whereas in the indeterminate, photoperiod-sensitive, spreading Vita 5 yield decreased with increasing N. Generally, biomass production of shorter component crops is reduced by depression of photosynthesis due to decrease in solar radiation by shading of taller component crops. From the available evidence, the following three cases can be assumed in terms of differences in plant height and canopy width between legume and non-legume in legume-based intercropping systems.

1) Component legume is taller than non-legume: The legume can grow well due to high photosynthetic activity and high BNF with adequate solar radiation, however, non-legume growth is severely suppressed due to depression of photosynthesis through decreases in irradiance. Under such conditions, biomass production of intercropping approaches that of monocropping of legume. It has been frequently observed that legumes such as soybean, develop large lateral leaves at higher positions and that most solar radiation can be intercepted by these leaves, so shading of shorter non-legume becomes intense (Fig. 1) (Fujita et al. 1990).

2) Non-legume is taller than legume: Growth of the non-legume is controlled not by solar radiation but by N nutrition status. Because the non-legume grows with a limited amount of N, its leaf area is small, and thus shading of shorter component legume by non-legume is not so severe, which results in greater biomass production and higher BNF in legume. This situation can be frequently observed in cereal/legume intercropping.

In such intercropping systems, BNF and N-transfer affect biomass production of cereal, particularly N transfer from legume to non-legume, because N-supply derived from the soil is not adequate and biomass production of the intercropping system is largely determined by that of the component non-legume (Fujita et al. 1990).

However, when abundant N-fertilizer is applied, plant height and biomass production of the non-legume can be accelerated, but that of the legume is reduced by shading, and biomass production of intercropping system approaches that of monocropping of the non-legume.

3) Legume and non-legume are at the same height: Competition for solar radiation between intercropped legume and non-legume is intense. As proposed for cassava/pigeonpea intercropping, canopy width may also control the amount of solar radiation received by a component crop (Cenpukdee and Fukai 1992 a and b). Compared with case 2), component legume could receive more solar radiation and express higher BNF. However, it has been observed that higher BNF does not always result in higher N-transfer (Ofosu-Budu et al. 1993b).

The above assumptions emphasize the importance of plant height and canopy structure of component crops in receiving solar radiation. However, biomass production efficiency of intercropping cannot be always determined by these two factors alone. We speculate that in some cases of intercropping combination, plant type should also be included to optimize the efficiency of canopy, which differs greatly between soybean and sorghum (Fig. 1). In soybean, light transmission ratio (LTR) abruptly decreases towards the

stem base probably due to development of many large lateral leaves at higher positions. In sorghum, however, LTR decreases more gradually downwards. When soybean is taller than sorghum , sorghum growth decreases tremendously due to severe shading by soybean.

If intercropped non-legumes or legumes have plant types like soybean, biomass production efficiency of the intercropping system could not exceed sole cropping of respective crops due to extremely poor growth of component shorter crops due to severe shading. In intercropping of cassava varieties differing in plant height relative to pigeonpea, Cenpukdee and Fukai (1992a) reported that in terms of economic yield of the intercrop, any cassava cultivars used did not show any advantage of intercropping over sole-cropping, as LER was about 1.0 or less.

From this evidence, it can be speculated that for improving biomass production in intercropping, plant type of the taller component crop plays an important role.

Cultural management

The influence on yield and production efficiency of component crop densities and manipulations of spacing between component crops, such as row arrangement and inter-row spacing, has been evaluated by Ofori and Stern (1987). They suggested that the cereal component was usually little affected by these manipulations, whereas the legume yield usually decreased significantly depending on the proximity of the cereal, perhaps due to the top of the legume canopy being shaded. However, these trials were mostly carried out using high levels of fertilizer-N, which promoted heavy leaf production, Ofori and Stern (1987) concluded that, although the cereal usually contributes a larger proportion of total yield, the legume seems to determine the magnitude of the intercropping advantage or efficiency.

Row arrangement and plant spacing

Overall mixture densities and proportions of component crops determine yields and production efficiency of cereal/legume intercrop systems (Willey and Osiru 1972). In systems with equal numbers of component crops, the more aggressive crop appears to determine productivity efficiency (Willey and Osiru 1972). When maize and cowpea were planted alternately in the same row rather than in alternate rows, grain yield and water use efficiency (WUE) were significantly higher. However, no difference in evapotranspiration was observed (Hulugalle and Lal 1986). Planting maize and cowpea in alternate rows did not affect maize yield, but planting cowpea in the same row with maize increased maize yield by 2.23%. This suggests that plant arrangement determines how effectively available resources are used, especially soil moisture.

Mohta and De (1980), from maize/soybean and sorghum/soybean intercropping trials, reported that cereal yields were little affected by intercropping with soybean, when arranged in either single or double alternate rows. The intercropped soybean yield increased 31% when component crops were arranged in double alternate rows rather than single rows.

In maize/soybean intercropping at different proportions and arrangements, Yunusa (1989) reported that reducing the maize proportion in the mixtures improved the soybean yield. Increasing the proportion of any component crop in the mixtures, up to 100% for maize and 67% for soybean, increased total yield. Fujita et al. (1990) reported that the proportion of dry matter contribution of sorghum was lower at 50 x 50 cm (40,000 plants ha^{-1}), but it increased with population density and surpassed the soybean contribution at spacing closer than 25 x 25 cm (160,000 plants ha^{-1}). This may be mainly due to the amount of light available to soybean. For instance, at a high population density (320,000 plants ha^{-1}), LTR at the top of soybean was below 40% (Fig. 1).

Intercropping efficiency increases with high population densities, as found in a sorghum/bean intercrop (Osiru and Willey 1972) and in a maize/cowpea intercrop (Fawus et al. 1982). The efficiency could be improved by reducing interspecific competition between component crops for limiting growth factors (Willey 1979). Ofori and Stern (1987) reported that the average legume component yield declined to 52% of the sole crop, whereas the cereal component yield decreased by only 11%. The LER was 1.91 without applied N and 1.43 at 120 kg N ha^{-1}.

Time of sowing

Relative yield of the legume component has been reported to increase if planted before the cereal component. According to Francis (1986), bean yield was reduced by more than 50% when maize was planted before the beans. However, when the legume component was planted 15 days earlier than the cereal, a higher yield was obtained. Ofori and Stern (1987), however, concluded that variation in time of sowing on intercrop yields has no advantage over simultaneous sowing. In staggered sowing, the earlier planted component has an initial advantage over the later planted component. At maturity, yield loss due to later sowing of the component crop could not be fully recovered.

Mandal et al. (1990) observed yield differences when various legumes and rice were intercropped simultaneously and when rice planting was deferred 30 days after the legume component. Yield differences among the various combinations were attributed to differences in growth habits, acquisition of nutrients, etc. It is apparent that each species, especially the legume's growth habits and plant architecture, must be considered when deciding to defer planting of any component crop.

Agronomic manipulation such as time of planting may have small effects on the performance of component crops in cassava/soybean intercropping (Thung and Cook 1979). However, agronomic manipulation in cassava intercropping may result in a large variation in yields of component crops when an aggressive, long-duration legume such as pigeonpea is used in intercropping. In such intercropping, cassava and pigeonpea compete for a long time, and that the competitiveness of the two species differs greatly between experiments (Cenpukdee and Fukai 1992a). Cenpukdee and Fukai (1992b) concluded that a vigorous cassava cultivar and late sowing of pigeonpea at a low density can sustain a desirable canopy width and competitiveness for high productivity of cassava/pigeonpea intercropping.

Fertility management

In cereal/legume mixed cultures, generally the relative competitiveness of component species changes with management practices such as fertilizer application and plant population, that are mostly associated with variations in the ability to compete for light (Rhodes and Stern. 1978). Even when light competition is not intense, heavy fertilization may inhibit the way the component crops complement each other's resource use (Hall 1978).

Nitrogen application

Ofori and Stern (1987) reviewed the influence of applied N on various intercropping systems. They found that intercrop cereal yields increased progressively with N application, whereas seed yield of legume either decreased or responded less. They concluded that N application did not improve LER and, thus, the efficiency of cereal/legume intercropping systems.

Searle et al. (1981) in a maize/groundnut intercrop with N application up to 100 kg N ha^{-1}, found that grain yield of intercropped maize increased progressively with increasing N application, whereas groundnut seed yields decreased. Intercropping efficiency measured by LER was 1.36 without fertilizer application and 1.24 at 100 kg N ha^{-1}. Similar phenomena have been observed in maize/cowpea systems (Ofori and Stern 1986).

Changes in crop yield and production efficiency caused by intercropping and combined-N application can be explained in terms of competition for N and light. Generally, the cereal component is taller and with its more extensive root system has a competitive advantage over the legume. A legume capable of fixing N_2 is thought to compete less with the cereal component for soil-N (Trenbath 1976).

When no N-fertilizer was added, strong competition between maize and cowpea for soil-N was observed (Chang and Shibles 1985; Ofori and Stern 1986). Strong interspecific competition between maize and cowpea was demonstrated by Ezumah et al. (1987). They suggested that inconsistent yields in intercropping may be attributed to varying growth habits and plant architectures (Koli 1975) of component crops or to fertilizer application management (Haizel 1974). Intercropped maize (*Zea maize* L.) and ricebean *(Vigna umbellata* [Thumb.] Ohwi and Ohashi) under a constant planting density of 8 maize and 16 ricebean per m^{-2} and varied levels of combined-N application under rainfed conditions was evaluated in Northern Thailand (Rerkasem and Rerkasem 1988). Combined-N application ranging from 0 to 200 kg N resulted in significantly higher dry matter, grain, and N yield of intercropped maize and ricebean as compared with their monocrop yield (relative yield). The intercrop's advantage was speculated to be associated with N nutrition, efficient use of mineral N by the maize crop, and enhancement of N- fixation in intercropped ricebean, thus making it less dependent on the depleted pool of soil-N (Rerkasem and Rerkasem 1988; Rerkasem et al. 1988).

Large N applications cause excessive vegetative growth of the cereal, and suppress the legume's yield in maize/cowpea intercropping (Ofori and Stern 1986) and in sorghum/soybean intercropping (Ogata et al. 1986). Ofori and Stern (1986) observed a

similar phenomenon in a maize/cowpea combination, when intercrop seed yield was significantly reduced by application of 25 kg N ha^{-1}. It appears that N application intensifies competition for light between component crops and suppresses growth of the legume.

Conclusion

The evidence presented here demonstrates that cereal/ legume intercropping is beneficial for increasing biomass production and economic yield not only in current cropping season but also in the subsequent crops. Biomass and grain production in intercropping is mainly controlled by light and nitrogen among various parameters. Light interception by the canopy varies depending upon combination of species intercropped. Nitrogen-transfer plays an important role on biomass production and part of its mechanism has been clarified in relation to VAM fungi etc., however, it has not been estimated quantitatively. Characteristics of genotypes favorable for intercropping should be clarified through studies on light interception, interaction of carbon and nitrogen in crops under intercropping.

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Pigeonpea-Based Cropping Systems in the Semi-Arid Tropics

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Abstract

Pigeonpea has a unique place in the cropping systems of the semi-arid tropics. Cropping systems involving pigeonpea are quite diverse and complex. Depending upon agro-ecological situations and domestic needs, pigeonpea is grown as a sole crop, mixed crop, intercrop, strip crop, alley crop, or ratoon crop.

Traditionally, over 90% of the pigeonpea in the semi-arid tropics is grown as a mixed crop or intercrop with cereals (e.g., sorghum, maize, pearl millet, rice), legumes (e.g., groundnut, soybean, urdbean, mungbean, cowpea) and commercial crops (e.g., cotton, castor, cassava). The genotypes used are generally indeterminate, tall, and of long duration. The system is primarily oriented to subsistence and multiple crop production. The indeterminate and long duration genotypes have good potential, good as postrainy season crops in irrigated and flood-prone areas. Postrainy season pigeonpea in sequence with maize, early rice, or millets has proved quite promising in north-east plains and central zones of India. Preliminary studies have also shown that long duration pigeonpea cultivars having resistance to wilt and sterility mosaic could be successfully used in alley cropping systems.

In recent years, the advent of short duration (100-160 days), high yielding and determinate genotypes has proved to be a landmark in pigeonpea improvement. This has led to introduction of pigeonpea as a sole crop in non-traditional areas under multiple cropping systems. The pigeonpea-wheat rotation has become very popular in the northwest plains and central zones of India and is likely to spread to other zones and to other countries having similar agro-ecological conditions. The short duration cultivars have also shown promise in multiple-harvest and ratoon management systems, particularly in southern India where winters are mild. A breakthrough in pigeonpea production is expected from commercial cidtivation of these genotypes in various cropping systems under good management conditions.

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Introduction

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is an important grain legume of the semi-arid tropics. It occupies about 3.44 million ha and produces 2.72 million t grains annually (Food and Agriculture Organization 1991). India is the major pigeonpea-producing country accounting for 91% of the global pigeonpea production. Kenya, Malawi, Tanzania, Uganda, Myanmar, and the Dominican Republic are other important pigeonpea-producing countries.

Pigeonpea remains an integral part of the dryland subsistence cropping systems of the semi-arid tropics. This can primarily be attributed to it being a deep-rooted and drought-tolerant grain legume that adds substantial amounts of organic matter to the soil and meets food and fuel requirements of agrarian populations. Pigeonpea is grown as a sole crop, mixed crop, intercrop, strip crop, alley crop, or ratoon crop. Traditionally, over 90% of the pigeonpea is grown as a mixed crop or intercrop with cereals, oilseeds, short duration legumes, and various commercial crops during the rainy season. Seeds of the component crops are either mixed together and broadcast (mixed cropping) or sown in rows with definite plant geometry (intercropping). The indeterminate long-duration genotypes have also been successfully introduced as a postrainy season sole crop in the flood-prone northeast plains of India and are likely to spread to areas of Nepal, Bangladesh, and Myanmar where rainy season pigeonpea is prone to water logging conditions (Ali 1990).

The development of short duration pigeonpea cultivars in recent years has led to the introduction of the crop in irrigated areas under multiple cropping systems. In India, about 0.50 m ha is under short duration pigeonpea. These genotypes have also shown promise under multiple-harvest and ratoon management systems, especially in those areas where winters are mild (Rao and Sachan 1988).

Cropping systems

The major cropping systems involving pigeonpea are mixed cropping or intercropping and double-cropping. Recently effort has been made to evaluate pigeonpea under multiple-harvest, ratoon management, and alley cropping systems. Rainfall pattern and geomorphological features of the region, duration and growth habits of cultivars, and domestic needs of the rural population primarily determine the type of cropping system.

Intercropping and Mixed Cropping

In southern Asia, over 90% of pigeonpea, mainly long-duration and medium-duration cultivars are grown in dryland areas in mixed cropping and intercropping systems. In irrigated areas of northwest plains and central region of India, short-duration cultivars are grown both as sole crops and intercrops. Traditionally, crop mixtures involving pigeonpea are highly complex and diverse. A large number of crops are grown together with pigeonpea in different proportions by mixing and broadcasting seeds of the component crops. This is primarily a risk-aversion practice with diversified production. The

intercropping systems developed in recent years is an improvement over traditional mixed cropping and aim at efficient use of production resources, enhanced productivity, and providing greater stability in production.

Depending upon agro-ecological conditions, pigeonpea is intercropped with cereals, oilseeds, short duration pulses and commercial crops in different regions. Among these, pigeonpea/cereal and pigeonpea/oilseed intercrops are most common.

Pigeonpea/cereal intercropping

The important intercrops are pigeonpea/sorghum, pigeonpea/pearl millet, pigeonpea/maize, Pigeonpea/minor millets, and pigeonpea/rice. The pigeonpea genotypes used in such pigeonpea/cereal intercropping systems are medium to long duration (200-280 days). In such systems, the cereal is generally considered as the main crop, and all management practices are centered around it. Efforts are made to maximize yield of cereal component, often at the expense of pigeonpea. In a well-managed pigeonpea/cereal intercrop, 80-90% of the yield of cereal and 40-50% of the yield of pigeonpea are generally obtained.

In India, pigeonpea/sorghum intercropping is widely practiced on medium to heavy, textured soils in dryland areas of southeastern Uttar Pradesh, Vidarbha, and Marathwada regions of Maharashtra, northern Karnataka, and Telengana and Rayalaseema regions of Andhra Pradesh. This intercropping system is also prevalent in the semi-arid tropics of Africa. Willey et al. (1981) reported that on deep Vertisols of peninsular India, sorghum/medium duration (200-220 days) pigeonpea intercrops were highly productive. The analysis of results from 80 experiments on sorghum/pigeonpea intercropping revealed that the system provides 90% of the equivalent yield of sole sorghum and 52% of the pigeonpea. Results from large number of experiments conducted under All India Co-ordinated Research Project for Dryland Agriculture (AICRPDA) during 1972-80 showed that pigeonpea/sorghum (90-100 days duration) is most productive on Vertisols of central and peninsular India (Ali 1985). The land equivalent ratio (LER) ranged from 1.17 to 1.55 (Table 1). Higher productivity and monetary return from pigeonpea/sorghum as compared with sole sorghum has also been reported by several workers (Umrani et al. 1984, Renganayaki and Subramanian 1992).

Pigeonpea/pearl millet intecroppping is practiced in the semi-arid and arid regions of northwestern and peninsular India and West Africa, particularly on light, textured soils. Pearl millet with its quick tillering and fast growth often suppresses pigeonpea, however, the total productivity from this system is higher than that from sole crops. Results of field experiments conducted under AICRPDA on Alfisols in peninsular India showed that pigeonpea/pearl millet (1:2 rows) system is highly efficient with an LER ranging from 1.38 to 1.81 (Table 1).

Pigeonpea/maize intercropping has limited scope due to competition between two components. However, this system is being followed in regions were maize is an important crops i.e., in some areas of northeastern Rajasthan and the Bihar plateau of India (Ali 1990), western Tarai regions of Nepal, uplands of Java, Sumatra and Sulawsi in Indonesia (Karsono and Sumarno 1987), and in Zambia (Kannaiyan et al. 1988).

In eastern India, pigeonpea is intercropped with upland rice. In this system, a full

Table 1. Productivity and land equivalent ratio (LER) of cereal/pigeonpea intercrops in dryland zones of India (AICRPDA, 1972-80). All intercrops grown with 2 rows of cereals to 1 row of pigeonpea

Location	Cropping systems	Grain yield ($t\ ha^{-1}$)		LER
		Main crop	Intercrop	
Jhansi	Sole sorghum	2.43		
	Sole pigeonpea	0.69		
	Sorghum + pigeonpea	2.28	0.42	1.55
Hyderabad	Sole sorghum	1.95		
	Sole pigeonpea	1.33		
	Sorghum + pigeonpea	1.20	0.73	1.17
Bijapur	Sole pearl millet	1.16		
	Sole pigeonpea	1.68		
	Pearl millet + pigeonpea	1.00	0.90	1.38
Sholapur	Sole pearl millet	1.80		
	Sole pigeonpea	2.13		
	Pearl millet + pigeonpea	1.83	1.69	1.81

Source: Ali (1985)

population of rice is generally maintained. The pigeonpea genotypes used are usually 250-280 days in duration. Chandra et al. (1992) reported that intercropping of rice cultivar "Ananda" (105 days duration) with pigeonpea cv. T 7 (270 days duration) is more productive and efficient (LER = 1.85) under upland conditions of Orissa, India, than either of the sole crops. Studies on intercropping of short duration pigeonpea genotypes with rice showed that this system causes considerable competition between component crops and is consequently it is not profitable over sole cropping (Pandhi et al. 1992).

Intercropping of fodder sorghum or pearl millet with long duration pigeonpea is practiced in Uttar Pradesh and Bihar, India, to meet fodder requirements of mainly dairy cattle. Due to high-population pressure of the fodder crop, pigeonpea growth is retarded in the initial stages, but due to early removal of fodder crops from the field, pigeonpea recovers fast and produces reasonably good yield. In the Bundelkhand region of India, sorghum is managed both for grain and fodder in pigeonpea/grain sorghum intercropping. At maturity, the cobs of sorghum are removed, leaving the green stalks that are harvested later in a phased manner over a 2-month period. Recent studies under the All India Co-ordinated Pulses Improvement Project (AICPIP) showed that in this system, pigeonpea yield is adversely affected because the green stalk of sorghum competes with pigeonpea both for soil moisture and light (Ali 1994a).

Pigeonpea/oilseed intercropping

This system is gaining considerable importance in view of increasing demand for vegetable oils and protein. The oilseed crops commonly intercropped with pigeonpea are groundnut, soybean, and sesame. In this system, both the component crops are considered important by the farmers.

Due to high monetary return and domestic needs, pigeonpea/groundnut intercropping is most common in Maharashtra, Andhra Pradesh, Karnataka, and Gujarat states of India, and dry zones of the Mandalay, Sagaing and Magway divisions of Myanmar. Higher productivity from pigeonpea/groundnut system has been reported by

several researchers (Rafey and Verma 1988; Yadvendra at al. 1989; Chikkanna et al. 1992). Willey et al. (1981) reported that in a pigeonpea/groundnut system, groundnut produced 82% and pigeonpea 85% equivalent yield of their sole crops. In this system, groundnut efficiently utilizes early-season resources owing to its rapid growth and expansive crop canopy. Even at later stages, when the pigeonpea develops sufficient canopy, groundnut appears to have the ability to efficiently use the reduced light intensity under the pigeonpea canopy.

Pigeonpea/soybean and pigeonpea/sesame intercropping are prevalent in dry areas of central India and also in Myanmar. In the Malwa and Bundelkhand regions of India, the pigeonpea/soybean system is fast replacing other pigeonpea-based intercrops due to higher stability and monetary return (Tomer et al. 1984; Patra & Chatterjee 1986; Vyas et al. 1992). On Alfisols of the Vindhyan range in India, Singh et al. (1993) observed that pigeonpea/sesame intercropping is highly remunerative. Reddy and Venkateswarlu (1992) studied the feasibility of pigeonpea/sunflower intercropping on Alfisols of peninsular India. They observed that intercropping two rows of sunflower between pigeonpea rows spaced at 120 cm gives 55% higher pigeonpea equivalent yield than sole crops, mainly due to efficient utilization of water under rainfed situations.

Pigeonpea/short-duration pulses intercropping

Short duration pulses, e.g., urdbean, mungbean, cowpea are intercropped with pigeonpea cultivars of all maturity groups in various parts of India and western Tarai of Nepal. In this system, pigeonpea is considered as the main crop and its full population is maintained. Multilocation studies under AICPIP during 1973 to 1985 showed that intercropping of short duration pulses provides 400-500 kg ha^{-1} bonus yield, with only a marginal decrease in pigeonpea yield and, consequently, the system is highly profitable as indicated by the monetary return shown in Table 2. Giri and De (1978) and Pandhi et al. (1992) reported that under good management conditions, intercropping of short-duration pulse crops do not depress pigeonpea yield.

Pigeonpea/commericial crops

This system involves intercropping of short-to medium-duration pigeonpea cultivars with long-duration crops like cotton, castor, and cassava.

In India, pigeonpea/cotton intercropping is practiced on Vertisols in some parts of the Central Zone, and pigeonpea/castor on Alfisols in the Peninsular zone. However, this system has only limited scope, because the monetary returns are not attractive as compared with sole cotton or castor. Reddy et al. (1993) studied the performance of different crops as an intercrop with pigeonpea in the Peninsular zone and found that castor is more remunerative than Italian millet but inferior to sorghum.

Sequential cropping

Double cropping with pigeonpea is relatively a new innovation. It has been made possible by the advent of high-yielding and short-duration genotypes, and the introduction of pigeonpea in non-traditional areas as a postrainy season crop. Pigeonpea- wheat sequential

Table 2. Productivity and monetary return from pigeon pea-based intercrops in various agro-climatic zones of India (1973-85 AICPIP)

Location	System		Grain yield (t ha^{-1})		Net return (Rs ha^{-1})
			Pigeonpea	Intercrop	
Pantnagar	Sole pigeonpea (cv.)	T21	2.31	-	4,576
	Pigeonpea + mungbean	2:1 RR[1]	2.07	0.52	5,206
	Pigeonpea + urdbean	2:1 RR	2.03	0.72	5,105
Hisar	Sole pigeonpea (cv.)	T 21	2.48	-	5,497
	Pigeonpea + soybean	2:2 RR	2.57	0.46	6,634
	Pigeonpea + mungbean	2:2 RR	2.30	0.38	6,406
Delhi	Sole pigeonpea (cv.)	Pusa Ageti	1.32	-	
	Pigeonpea + mungbean	1:1 RR	1.19	0.62	NR[2]
Ludhiana	Sole pigeonpea (cv.)	AL15	1.25	-	
	Pigeonpea + mungbean	2:1 RR	1.16	0.38	
	Pigeonpea + urdbean	2:1 RR	1.15	0.26	NR
Bangalore	Sole pigeonpea (cv.)	Hy 3C	1.60	-	
	Pigeonpea 4- urdbean	2:1 RR	1.57	0.51	
	Pigeonpea + cowpea	2:1 RR	1.46	0.61	NR

1 RR: Row ratio
2 NR: Not reported

Source: Ali (1985)

cropping has become quite popular in the irrigated areas of northwestern and Central India (Chandra and Ali 1986). In dryland areas of Myanmar also, short-duration pigeonpea has paved the way for double cropping (Kyaw Moe 1989). Postrainy season pigeonpea has shown great promise in the double cropping system in eastern and peninsular India (Roy Sharma et al. 1981; Srivastava et al. 1988) and has potential for adoption in Nepal and Bangladesh under similar agro-climatic conditions.

Pigeonpea-cereal sequential cropping

This system involves pigeonpea and wheat. It is prevalent in the irrigated areas of Haryana, Punjab, Uttar Pradesh, Gujarat, Madhya Pradesh, and Maharashtra states of India. Early-maturing genotypes of pigeonpea (140-170 days) are planted by mid June with pre-sowing irrigation. The crop is harvested by November and the wheat is harvested after this. The land area under pigeonpea-wheat sequential cropping is progressively increasing. Other post rainy season crops e.g., barley, lentil, chickpea, and sunflower, may also follow pigeonpea. Results of multilocational AICPIP trials showed that pigeonpea-wheat sequential cropping is highly productive in northern India (Table 3). The yield of pigeonpea ranged from 1.7 to 2.1 t ha^{-1} and wheat from 2.9 to 5.3 t ha^{-1}.

Cereal and postrainy season pigeonpea sequential cropping

In eastern India where pigeonpea sown in the rainy season often suffers heavy losses due to excessive rains and frequent floods, introduction of pigeonpea as a postrainy season crop has provided a promising alternative for increasing pigeonpea productivity. Postrainy season pigeonpea was initially introduced in northern Bihar with development of the long duration variety "Bahar". Subsequently, this variety was attacked by Alternaria blight,

Table 3. Yield and monetary return from pigeonpea-wheat sequential cropping in northern India

Location	Yield (t ha^{-1})		Net return
	Pigeonpea	Wheat	(Rs. ha^{-1})
Hisar	1.74	4.10	8,223
Dholi	1.75	2.86	7,550
Kanpur	2.11	5.34	15,811

Source: Chandra and Ali (1986)

which setback the postrainy-season pigeonpea. In recent years, development of two new varieties resistant to alternaria blight and sterility mosaic disease (SMD) e.g., Sharad and Pusa 9, has renewed the promise for postrainy-season pigeonpea production. The land area under this crop is rapidly increasing. In eastern India, postrainy season pigeonpea generally follows maize, fodder sorghum, pearl millet and early rice. In northern Bihar, pigeonpea grown in sequence with maize gave 3.43 t seed yield ha^{-1} (Roy Sharma et al. 1981). Among various crop rotations, maize-pigeonpea with a net return of Rs. 7552 ha^{-1} was found to be most remunerative followed by maize-peas and maize-mustard. Cereal and postrainy-season pigeonpea double-cropping has also strong potential in Bangladesh, Nepal, and Myanmar.

Ratoon Cropping

In this system, pigeonpea is managed for multiple-harvest by harvesting pod-bearing branches or hand picking of pods at maturity of the first flush and allowing the crop to regenerate. The concept of multiple-harvest is advocated by ICRISAT due to development of a short-season genotype (ICPL 87) and growing it at a high-population density. Chauhan et al. (1987) reported 4.1 to 5.2 t seed yield ha^{-1} from ICPL 87 under good management in three harvests during a growing period of 220 days. Rao and Sachan (1988) observed that even under rainfed conditions, ratoon cropping of ICPL 87 is quite successful. On Alfisols, the yield of ICPL 87 in three harvests (by picking pods) was 2.5 t ha^{-1}, compared with 1.33 t ha^{-1} from a medium duration genotype.

Subsequent multilocational studies under AICPIP revealed that ratoon cropping is economically viable only under irrigated conditions in peninsular India (Rahuri) where winters are mild. In northern India, where the pigeonpea-wheat rotation is becoming popular, ratoon cropping of pigeonpea is not encouraging (Table 4) due to low winter temperature. Further more, the ratoon crop may serve as a potential source for the inoculum of SMD.

Alley Cropping

Perennial pigeonpea is receiving considerable attention as a multipurpose woody species for agroforestry systems due to its fast growth, woody and hardy nature, and ability to survive well under dryland conditions. In this system, several rows of pigeonpea are grown as a hedge row and food crops are sown in the alleys. At the termination of the first

Table 4. Total seed yield (t ha^{-1}) of pigeonpea under ratoon cropping at different population density. Mean of 1984-85 to 1986-87 AICPIP trials

Population density (10^3 plants ha^{-1})	Southern India			Northern India
	Rahuri (N 290-21)	Badnapur (BDN 2)	Bangalore (Hy 3C)	Varanasi (Bahar)
	Ratoon Crop			
80	1.73	0.64	-	0.84
160	2.06	0.76	-	1.01
240	2.40	0.99	1.77	-
320	2.48	1.28	-	1.33
400	2.33	1.18	-	-
480	2.22	0.83	-	1.38
	Non-ratoon crop			
	1.63	1.90	2.49	1.77

year, pigeonpea crop is ratooned at a 0.5 to 1.0 m height and the plants are allowed to regenerate. In subsequent years, side branches of pigeonpea are removed to reduce competition with food crops.

Ali (1994 b) evaluated five genotypes of long duration pigeonpea under alley cropping on Inceptisols of Uttar Pradesh during 1989-91. The intercrops were fodder sorghum during the rainy season and mustard during the winter season. This system was compared with a traditional system of pigeonpea/sorghum mixed cropping on an annual basis. Results showed that at the termination of a 2-year cycle, alley cropping with ICP 6443 and ICP 8860 proved more beneficial under rainfed conditions than annual system of pigeonpea/sorghum mixed cropping. Alley cropping with ICP 8860 provided 1.9 t pigeonpea grain, 14.3 t dry sticks, 6.1 t green leaves, 77 t fodder sorghum dry matter, and 0.4 t oilseeds ha^{-1} (Table 5).

Studies on Alfisols at Jhansi during 1991-93 showed that the pigeonpea/groundnut system of alley cropping gives higher yield than a pigeonpea/grain sorghum system. The yield potential of pigeonpea increases after first ratooning under pure and alley systems (Newaj et al. 1994). However, information on feasibility as well as economic viability of pigeonpea-based alley cropping systems for different agro-ecological conditions are meager. Further more, the mortality of plants in subsequent years due to termites and hot winds during summer months, and also because the perennial crop is as a source of some disease inoculum, may pose problems in wider acceptability of the system.

Management systems

Intercropping

The success of an intercropping system largely depends upon selection of compatible crops and their genotypes, appropriate planting geometry, and judicious use of production inputs.

Table 5. Yield under a perennial pigeonpea production system (total yield over 2 years)

Treatments	Pigeonpea			Sorghum	mustard	Gross monetary
	Grain	Dry stick	Green leaves	fodder	(dry matter)	return (Rs. ha^{-1})
		(tha^{-1})		(tha^{-1})		
Genotypes						
ICP 6443	1.98	16.42	5.92	7.68	0.32	43,487
ICP 8094	1.79	17.48	5.86	7.44	0.37	42,490
ICP 11289	1.34	14.43	4.47	7.76	0.34	37,403
ICP 8860	1.95	14.34	6.17	7.76	0.42	43,294
Bahar	1.77	14.10	5.85	7.72	0.39	41,389
Traditional system (pigeonpea /sorghum mixture)	2.98	8.08	-	6.31	-	40,524
LSD (p=0.05)	2.20	0.61		0.31		
Alley width (m)						
2.5	1.98	17.33	5.86	7.46	0.34	43,695
3.0	1.71	14.08	5.44	7.88	0.40	41,122
LSD (p=0.05)	0.09	0.27	-	0.14		

1 Sale rate (Rs. kg^{-1}): Pigeonpea grain 8.00 ; pigeonpea stick 0.50 sorghum fodder (dry matter) 2.00 ; pigeonpea green leaves 0.20

Sources: Ali (1994 b)

Genotypic compatibility

Identification of suitable genotypes of the component crops is necessary for complementarity. The duration, growth rhythm, canopy structure, and rooting pattern are the major considerations in selection of genotypes. Genotypes that give high yields in sole cropping are not necessarily the highest yielding in intercropping (Rao et al. 1981). In multilocational trials to evaluate pigeonpea genotypes for intercropping with sorghum, short duration genotype T 21 suffers more loss in an intercropping system as compared with long-duration genotypes at Sehore (Table 6). At Parbhani, some genotypes in an intercropping system produce yield almost identical to that in sole cropping (Ramanujam 1981). Verma et al. (1992) reported that in pearl millet hybrid HHB 67 is more compatible than HHB 50 for intercropping with pigeonpea. Similarly, in a rice/pigeonpea intercropping system, pigeonpea cultivar T 7 (270 days) and rice genotypes "Ananda" (105 days) are more compatible than other combinations of genotypes (Chandra et al. 1992).

Planting geometry

Planting pattern varies considerably in different regions and intercropping systems. The traditional broadcast system is difficult to manage. An improvement over this system is row planting in which either full population of the main crop is maintained (additive series) or one or two rows of the main crop are omitted to accommodate intercrops (replacement series). Bajpai and Singh (1992) working on different pigeonpea based intercropping systems found that line sowing is distinctly superior to broadcasting. The net gain in monetary return by line sowing over broadcast was Rs. 1387 ha^{-1} (Table 7). However, various intercrops i.e., rice, kodomillet, urdbean, and maize did not show differential response to planting methods.

Table 6. Genotypic compatibility of pigeonpea intercropped with sorghum

Location	Genotype	Pigeonpea yield (t ha^{-1})		Reduction in intercrop compared with sole crop (%)
		Sole	Intercrop	
Sehore	Gwalior 3	1.22	0.88	28
	No. 148	0.75	0.27	64
	T 21	0.42	0.14	67
	NP (WR) 15	1.35	0.73	46
Gwalior	NP(WR)15	0.85	0.57	33
	K 28	0.88	0.43	51
	AS 29	0.98	0.90	8
	K 23	1.11	1.07	4
Parbhani	No. 56-30	1.12	1.11	1
	BDN 1	0.87	0.88	-21[1]
	No. 56-45	1.09	1.21	-11
	No. 38	0.63	0.84	-33

1 Negative sign indicates higher yield under intercropping

Source: Ramanujam (1981)

Table 7. Grain yield and net return of pigeonpea and intercrops as affected by cropping systems and method of sowing

Treatments	Grain yield (t ha^{-1})			Net return (Rs. ha^{-1})
	Pigeonpea	Intercrops	Pigeonpea equivalent	
Intercropping systems				
Sole pigeonpea	1.62	-	1.62	8,939
Pigeonpea/rice	1.42	0.07	1.44	7,098
Pigeonpea/kodo millet	1.02	1.10	1.23	5,788
Pigeonpea/urdbean	1.15	0.20	1.81	10,263
Pigeonpea / maize	1.30	1.72	1.83	10,586
LSD 5%	0.20	0.21	0.27	
Method of sowing				
Line sowing	1.39	0.83	1.48	7,680
Broadcast	1.22	0.72	1.30	6,293
LSD 5%	0.09	NS	0.15	

Source: Bajpai and Singh (1992)

In additive systems, either intercrops are sown between normally spaced rows of the base crop, such as in pigeonpea/short duration pulses, or rows of tall-growing component crops like pigeonpea, sorghum, or pearl millet are paired at 50% of the normal distance, leaving a wide space between paired rows so as to accommodate one or two rows of an intercrop. Paired row planting allows more radiation for the smaller-statured component crops and minimizes competition for light. Giri et al. (1981), working on pigeonpea/groundnut intercropping at Badnapur (Maharashtra), found that by pairing rows of pigeonpea at 30/70 cm the yield of groundnut increases by 0.48 t ha-1 over uniform row planting (Table 8).

Low plant population has been generally recognized as a limiting factors of higher productivity in intercropping systems. The multilocational studies under AICRPDA clearly

Table 8. Yield of pigeonpea/groundnut intercrops as influenced by planting geometry (Badnapur, Maharashtra)

Cropping systems	Yield (t ha^{-1})		
	Pigeonpea	Groundnut	Pigeonpea equivalent
Pigeonpea sole uniform row (50 cm)	1.02	-	1.02
Pigeonpea sole paired row (30/70 cm)	0.95	-	0.95
Pigeonpea (50 cm)/ Groundnut (1:1 RR[1])	0.93	0.81	1.52
Pigeonpea (30/70 cm)/ Groundnut (2:2 RR)	0.95	1.29	1.90

1 RR: Row ratio

Source: Giri et al (1981)

revealed that higher productivity from pigeonpea/sorghum intercropping is obtained when optimal population of both crops (180,000 plants ha^{-1} for sorghum and 40,000 plants ha^{-1} for pigeonpea) are maintained under a 2:1 row arrangement (Venkateswarlu et al. 1979).

Adjustment in the planting time of the component crops may also enhance productivity. Yadvendra et al. (1989) reported that relay intercropping of pigeonpea with groundnut on deep Vertisols of the Saurashtra region, Gujarat, India only marginally decreases yield of groundnut, and under favorable conditions, the yield of pigeonpea is similar to that of a normally sown crop.

Fertility management

Despite the fact that pigeonpea is generally grown under intercropping or mixed cropping systems, studies on fertilizer use have mainly been conducted on sole crops. Only in recent years has there been a shift in fertilizer use research now focussing on pigeonpea based cropping systems. Fertilizer requirement of an intercrop depends upon the nature of component crops and their population densities. In a system involving legumes and non-legumes, moderate levels of applied-nitrogen (N) appears more advantageous (Narain et al. 1980). At higher levels of N, nodulation of the legume component adversely affected and the cereal crop would have to depend mainly on applied-N.

On the basis of multilocational trials conducted on fertilizer management in pigeonpea/sorghum intercropping under AICPIP, application of full dose of N and phosphorus (P) (60:40) to cereal component is adequate to meet the nutrient requirement of pigeonpea (Ali 1992). Venkateswarlu and Ahlawat (1986) also reported that under dryland conditions, application of N and P only to cereal component in pigeonpea/sorghum intercropping, is more beneficial. Palaniappan et al. (1984), however, reported that the P requirement of pigeonpea/legume intercropping is higher than sole pigeonpea.

Weed management

The nature and magnitude of crop-weed competition differs considerably between sole and

intercropping systems. The crop species, population density, sowing geometry, duration, and growth rhythm of the component crops, the moisture and fertility status of soil, and tillage practices influence weed flora in intercropping systems.

Ali (1988) reported that in pigeonpea-based intercropping, legumes (cowpea, urdbean and mungbean) suppress weed flora by 30 to 40% compared with 22% by sorghum. Studies on crop-weed competition revealed that the critical period for weed control in intercropping systems is slightly longer than that for sole crops. Sole sorghum needs weed free conditions for the initial 4-5 weeks, whereas in sorghum/pigeonpea intercrops, this period has to be extended upto 7 weeks. Multilocational studies under AICPIP during 1984-87 revealed that in a short duration pigeonpea/mungbean or urdbean intercropping, the initial 30 days is most critical for weed control (Table 9). The uncontrolled weeds upto 15, 30,45, and 60 days of sowing caused yield loss of 13, 23, 31 and 35% respectively, over a weed-free control. In a long duration pigeonpea/sorghum system, the critical period of crop-weed competition extended up to 8-9 weeks (Ali 1991).

Manual weeding is the most common method of weed management in pigeonpea-based intercrops. In broadcast sowing, weeding is also done by running a country plough at 40-50 cm spacing 4-6 weeks after sowing. However, this offers only partial control of weeds and also causes some damage to crops. Relatively little work has been done on screening suitable herbicides for pigeonpea-based intercrops. In Inceptisols at Kanpur, pre-emergence application of pendimethalin (1.5 kg ha^{-1}) proved quite effective in controlling weeds in a pigeonpea/sorghum intercropping system (Table 10). In pigeonpea/short duration legumes, fluchloralin (0.5 to 0.75 kg ha^{-1}) and alachlor (2 kg ha^{-1}) have been reported to effectively control seasonal weeds (Venkateswarlu and Ahlawat 1986) and enhance productivity

Planting time and genotypes in sequential cropping

Planting time and choice of appropriate genotypes play a key role in determining the success of pigeonpea-wheat systems. The ideal time of planting of short-duration pigeonpea is by mid-June. Late planting not only endangers timely sowing of wheat but

Table 9. Productivity of pigeonpea + mungbean/urdbean intercropping system as influenced by crop-weed competition (1984-87 AICPIP)

Treatments	Grain yield (t ha^{-1})			Loss in yield compared with weed free (%)
	Pigeonpea	Intercrop	Total	
Weed-free until 15 days of sowing	0.78	0.29	1.07	31.2
Weed-free until 30 days of sowing	0.79	0.39	1.17	24.8
Weed-free until 45 days of sowing	1.07	0.49	1.56	-
Weed-free until 60 days of sowing	1.12	0.39	1.50	3.6
Unweeded until 15 days of sowing	0.99	0.36	1.35	13.3
Unweeded until 30 days of sowing	0.86	0.34	1.21	22.7
Unweeded until 45 days of sowing	0.78	0.30	1.08	30.6
Unweeded until 60 days of sowing	0.71	0.31	1.02	34.7
Weed-free until maturity	1.17	0.39	1.56	-
Unweeded until maturity	0.58	0.23	0.82	47.7

Source: AICPIP studies 1984-87.

Table 10. Effect of herbicides on yield of a pigeonpea/sorghum intercrop

Treatments	Grain yield (t ha^{-1})		
	Pigeonpea	Sorghum	Pigeonpea equivalent
Alachlor 1 kg ha^{-1}	1.94	0.73	2.17
Alachlor 1 kg ha^{-1} + one HW[1] 30 DAS[2]	2.19	0.84	2.45
Alachlor 2 kg ha^{-1}	2.16	0.73	2.39
Isoproturon 0.75 kg ha^{-1}	1.98	0.72	2.29
Isoproturon 0.75 kg ha^{-1} + one HW 30 DAS	2.07	0.79	2.31
Isoproturon 1.5 kg ha^{-1}	1.90	0.89	2.14
Benthiocarb 0.75 kg ha^{-1}	1.90	0.74	2.12
Benthiocarb 0.75 kg^{-1} + one HW 30 DAS	2.02	0.74	2.25
Benthiocarb 1.5 kg ha^{-1}	1.86	0.72	2.08
Pendimethalin 0.75 kg ha^{-1}	2.25	0.74	2.47
Pendimethalin 0.75 kg ha^{-1} + one HW 30 DAS	2.21	1.10	2.54
Pendimethalin 1.5 kg ha^{-1}	2.41	0.83	2.66
One HW 20 DAS	2.10	0.83	2.35
One HW 20 and 45 DAS	2.24	0.91	2.52
Unweeded control	1.66	0.64	1.85
Weed free control	2.44	1.16	2.79
LSD 5%	0.19	0.08	0.14

1 DAS = Days after sowing
2 HW = hand weeding

Source: Ali (1991)

also results in low yield due to poor plant stand and limited biomass production. At Ludhiana, Punjab state of India, the first fortnight of June was found to be an optimal planting time for pigeonpea in pigeonpea-wheat rotation (Kaul et al. 1980; Sandhu et al. 1981). For genotypes of T 21 group maturity (170-180 days), April planting has been found quite promising, especially in those areas where summer mungbean is cultivated. Panwar and Yadav (1981) reported that pigeonpea (T 21) planted 15 April produced 3.6 t ha^{-1} grain yield compared with 1.7 t ha^{-1} for pigeonpea. Further more, the yield of succeeding wheat after April-planted pigeonpea was 6.7 t ha^{-1} whereas it was only 5.3 t ha^{-1} after June-planted pigeonpea.

Information on the effect of different pigeonpea genotypes on total productivity in pigeonpea-wheat rotation is meager. The extra short-duration (120-140 days) varieties, although the wheat was timely sowed, had lower yields and also added less biomass to the soil than short-duration ones. Srivastava et al. (1988) evaluated four genotypes of pigeonpea (ICPL 87, ICPL 151, ICPL 161, and UPAS 120) in a pigeonpea-wheat rotation at Gwalior, Madhya Pradesh state of India, and reported that ICPL 87 and ICPL 151 are more suited than other genotypes in pigeonpea-wheat rotation. However, in view of a little longer duration of ICPL 87 (160-180 days), they recommended ICPL 151 for double crop system. In Uttar Pradesh, Punjab and Haryana states of India, the short-duration varieties e.g., UPAS 120, AL 15, Manak are considered ideal for double cropping.

One prerequisite for achieving higher productivity from postrainy season pigeonpea is timely planting. The first fortnight of September appears to be ideal for planting in the northeast plains of India. Results from experiments conducted under AICPIP during 1982-

83 revealed that at Dholi, in Bihar state of India, variety MA 128-2 yielded 2.0 t yield ha^{-1} when planted on 1 September, but when planted on 21 September its yield was only 0.27 t ha^{-1}. Similarly at Akola, Maharashtra state of India, variety C 11 produced 1.8 t seed ha^{-1} when planted on 25 September, but only 0.68 t ha^{-1} when planted on 30 October.

After rainy season cereals, planting of pigeonpea is often delayed, and consequently, desired productivity is not achieved. To overcome this problem, relay sowing 2 to 3 weeks before the harvest of the previous crop has been suggested (Khatua et al. 1977). At ICRISAT Asia Center, 20 days overlap with maize or sorghum increased pigeonpea yield from 0.7 to 0.99 t ha^{-1}. However, relay sowing poses practical difficulties, and a more realistic solution would be to develop cultivars that can be successfully planted late.

Future thrust

1. In the traditional cropping systems of the semi-arid tropics, pigeonpea will continue to be an important crop, especially in intercropping situations. The indeterminate, tall, and long duration genotypes are well adapted to limitations of moisture and nutrients, and thus *impart greater* stability *in* production system when intercropped with short season *cereals,* oilseeds, or other upland crops. Conventional intercropping is, however, oriented towards survival and diversified crop production rather than higher productivity.
2. Refinement of management practices and selection of component crops and genotypes by matching them to rainfall patterns, soil conditions, and length of growing season may considerably improve productivity of pigeonpea in intercropping systems. Greater stability in production is expected from the new genotypes that are resistant to SMD, wilt, and pod-borer complex. This may also encourage alley cropping and multiple harvesting.
3. A better understanding of complementarity of associated crops, moisture use, nutrient needs, soil health, and pest management in intercropping systems is needed to achieve higher productivity and stability. Pigeonpea/sorghum, pigeonpea/maize, and pigeonpea/groundnut are by far the most popular intercrop combinations in southern Asia and in Africa. Special attention should be paid to analyzing production constraints in these intercrops, and attempt to alleviate them.
4. The advent of early maturing (120-160 days), high yielding , and determinate genotypes in the recent past is a landmark in pigeonpea improvement. Efforts to identify extra-short duration and high-yielding genotypes with high harvest index should be continued so as to bring more area under pigeonpea-wheat sequential cropping. The productivity, stability, and sustainability of such cropping systems e.g., cereal-cereal rotation, should be further studied.
5. Post-rainy season planting has excellent potential for pigeonpea production in areas where heavy monsoon showers and floods may cause failure of the rainy season crop. Appropriate agronomic management practices need to be developed to popularize this cropping systems.

6. Development of extra-short duration, photo period, insensitive, and high-yielding genotypes having tolerance to excess moisture may help in bringing a considerable area of rice fallows under pigenpea. This may also allow relay cropping. In-depth studies on management aspects of these potential cropping systems should be pursued.
7. Long duration pigeonpea with perennial behavior could be introduced in agro-forestry systems by developing appropriate genotypes and management practices. More detailed information on identification of appropriate genotypes and their management systems is needed.

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Yield Advantages and Economic Returns from Pigeonpea/Cotton Strip Intercropping Rotations on a Vertisol in the Indian Semi-Arid Tropics

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Abstract

Pigeonpea (*Cajanus cajan (L.) Millsp.*) *is an important component of several cropping systems of the semi-arid tropics* (*SAT*). *In a 4-year field study* (*1990 to 1994*), *a medium duration pigeonpea, cultivar ICPL 87119 was strip-intercropped with hybrid cotton, cultivar NHH 44 in five replacement series of four strip widths* (1.5, 3, *4.5, and 6-m strip*) *under three land-configuration systems Iflat, ridge and furrow* (*RF at 0.75-m*), *and broadbed and furrow* (*BBF at 1.5-m*)] *on a Vertisol under rainfed conditions at ICRISAT Asia Center* (*IAC*), *Patancheru, India, A strip plot design was used with land configuration treatments allocated to vertical plots and cropping systems to horizontal pilots with three replications. Each crop strip was rotated with an associated intercrop in a 2-year rotation cycle. Land configuration treatments remained unchanged during the four years.*

Individual crop yields (*grain or seed cotton and stem dry matter*) *were significantly influenced by the cropping system but not by land configuration or treatment interactions. Seed cotton yields were higher than pigeonpea grain yields. Pigeonpea dry stem yields were higher than cotton stem yields during all four years. Sole pigeonpea grain yield varied from 0.49 to 1.57 t ha^{-1}, whereas sole seed cotton yield varied from 1.45 to 2.04 t ha^{-1}. Crop yields decreased as strip size was reduced, with greater yield reductions in cotton than in pigeonpea. Sole pigeonpea produced more total dry matter* (*TDM*) (*6.51 t ha^{-1}*) *than sole cotton* (*4.95 t ha^{-1}*). *Cropping system TDM production increased as pigeonpea strip size was increased. Land equivalent ratio* (*LER*) *and monetary value equivalent ratio* (*MVER*) *indicated that strip intercropping was always superior to sole cropping. A strip intercropping combination of 4.5-m pigeonpea and 1.5-m cotton gave the maximum mean LER value* (*1.4*) *and MVER value* (*1.19*). *Averaged over four years, sole cotton had the maximum gross* (*Rs. 19.87 thousands ha^{-1}*) *and net monetary returns* (*Rs. 14.25 thousands ha^{-1}*), *and sole pigeonpea had the lowest gross* (*Rs. 12.41 thousands ha^{-1}*) *and net monetary returns* (*Rs. 7.24 thousands ha^{-1}*). *All strip intercropping systems were more profitable than sole pigeonpea with maximum net returns* (*Rs. 9.97 thousands ha^{-1}*) *obtained from a strip intercropping combination of 1.5-m pigeonpea and 4.5-m of cotton. Benefitxost ratio varied widely among cropping systems and between years. However, sole cotton gave the maximum benefitxost ratio of 2.57,follozved by sole pigeonpea with a value of 2.18. Results of combined yield analysis of each rotation cycle, indicated the sole pigeonpea -*

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sole cotton rotation as the most profitable system when compared with strip intercropping combinations.

Introduction

Intercropping is a widespread practice in tropical developing countries. This system of cropping can offer potential advantages over sole cropping. Intercropping is the growing of two or more crop species simultaneously on the same field (Andrews and Kassam 1976). There are several types of intercropping systems including mixed, row, strip, and relay (Francis 1986). Strip intercropping is a system in which two or more crops are grown simultaneously in different strips narrow enough to develop inter-crop interference, yet with the advantage of facilitating independent crop management. There has been renewed research interest in strip intercropping in Canada (Fairey and Lefkovitch 1990), China (Zhongmin and Guang 1990), and the U.S.A. (Cruse 1990; Putnam and Allan 1992; West and Griffith 1992).

Vertisols are potentially the most productive soils in India and contribute significantly to the national economy (Murthy 1988). However, large amounts of the available 73 million ha of Vertisols are underutilized primarily because of inherent management and nutrition-related constraints. Vertisols are traditionally fallowed during the rainy season because these soils are non-trafficable when wet and non-workable when dry (El-Swaify et al. 1985). For such soils, the "watershed-based cropping systems approach" developed at ICRISAT allows cropping both during the rainy season (kharif) and the following dry and cool postrainy season (rabi). Improved cropping systems, graded broadbeds and furrows (BBF), and improved soil fertility are the main components of this Vertisol technology. The BBF system improves drainage and soil workability in such soils (Kampen 1980). Use of different land configuration systems (e.g., ridge or raised beds) have been found beneficial for several crops grown on poorly drained soils (Kumar et al. 1987; Mascagni and Sabbe 1990a and 1990b; Mascagni et al. 1991). However, little is known about the possible advantages of strip intercropping under different land configuration systems on Vertisols.

Intercropping and sequential cropping that involve short-duration and high yielding crop cultivars are the main components of the improved cropping systems. Although these cropping systems are characterized as highly productive and more efficient than traditional cropping systems, the focus in their development has been ICRISAT mandate crops in food-oriented production systems. There has been relatively little effort made to develop cash-oriented production systems involving crops like cotton - the most important cash crop grown on Vertisols by Indian farmers.

Pigeonpea (*Cajanus cajan* (L.) Millsp.) is an important component of several cropping systems of the semi-arid tropics (SAT). In India, pigeonpea is the most widely grown legume (3.62 million ha) next to chickpea (7.41 million ha), and contributes about 90% of the world production. Cotton (*Gossypium* spp.) is one of the most important cash crops grown in India. It is grown over an area of 7.36 million ha, with a production of about 9.76 million bales lint (each bale is 180 kg) annually. Traditionally, 80-90% of pigeonpea in India is intercropped with cereals (maize, sorghum, rice, and pearl millet), short-duration

legumes (green gram, black gram, and cowpea), oilseeds (groundnut, sesame, and castor), cotton, and cassava (Aiyer 1949). Pigeonpea/cotton intercropping is a major cash cropping system widely practiced on black cotton soils (Vertisols) of the Deccan Plateau in India. Farmers in this area usually plant several rows of cotton with a strip of sorghum or pigeonpea, either in distinct rows or in mixed cropping (Rao 1986). The average productivity of these cropping systems in farmers' fields is relatively low [pigeonpea = 0.66 t ha^{-1} grain and cotton = 0.65 t ha^{-1} seed cotton (Fertilizer Association of India (FAI) 1994)] when compared with yields obtained in experimental fields [pigeonpea = 2.5 t ha^{-1} grain (ICRISAT 1989) and cotton = 3 t ha^{-1} seed cotton (Basu et al. 1992)]. The primary reasons for these poor on-farm yields are: pest and disease susceptible cultivars, occurrence of intermittent drought and waterlogging conditions, and poor agronomic practices. The availability of high yielding disease and pest tolerant crop genotypes have improved the scope for pigeonpea/cotton intercropping.

Experimental

To evaluate the agronomic performance and economic returns of pigeonpea/cotton strip intercropping rotations under different land configuration systems, a field study was undertaken at ICRISAT Asia Center (IAC), Patancheru, India (17°N, 78.5°E and 500 m altitude) on a Vertisol during four cropping seasons (1990 to 1994) under rainfed conditions. Five strip-intercropping rotations with pigeonpea and cotton were evaluated under three land-configuration systems: flat, ridge and furrow (RF at 0.75-m), and broadbed and furrow, (BBF at 1.5-m). A medium-duration (180-200 days), high yielding pigeonpea, cultivar ICPL 87119, was strip-intercropped with a widely adapted hirsutum hybrid cotton, cultivar NHH 44, in five replacement series (4:0, 3:1, 2:2, 1:3, and 0:4) of four strip-widths (1.5, 3, 4.5, and 6-m strips). Each crop strip was rotated with the associated intercrop in a 2-year rotation cycle. A strip-plot design was used with land configuration treatments allocated to vertical plots and cropping systems to horizontal plots with three replications. Land configuration treatments remained constant during all four years. In each year, crops were grown with recommended crop management practices and insecticide sprays. Soil at the experimental site was low in mineral nitrogen (19.2 mg kg^{-1} NO_3 + NH_4^+ N) and available phosphorus (6.5 mg kg^{-1} available Olsen P) and rich in exchangeable potassium (135.9 mg kg^{-1} exchangeable K). Exchangeable K was estimated by using the method of Thomas (1982), mineral N by the method of Keeney and Nelson (1982), and available Olsen P by the method of Olsen and Sommers (1982). Total rainfall during each experimental period was 692 mm in 1990/91, 709 mm in 1991/92, 709 mm in 1992/93, and 776 mm in 1993/94. Rainfall was well distributed in all the cropping periods, except in 1992/93 where most rainfall occurred before August. Severe waterlogging did not occur in any of the cropping seasons. *Helicoverpa armigera* was the major pest, with high infestation observed in 1990/91 and 1992/93 cropping seasons. At maturity, each crop was harvested from a plot area (6 m x 4 m) and the dry yields recorded. Total crop duration varied from 213 days in 1993/94 to 259 days in 1990/91 for pigeonpea, and 216 days in 1990/91 to 269 days in 1993/94 for cotton.

Pigeonpea seed yield response

Pigeonpea seed yield responded significantly to strip widths but not to land configuration or treatment interaction (Table 1). Sole pigeonpea seed yields varied from 0.49 t ha^{-1} in 1992/93 to 1.57 t ha^{-1} in 1991/92. Intercropped pigeonpea consistently yielded better than expected yield of sole pigeonpea because of reduced intraspecific competition among pigeonpea plants. The yield from strip intercropping combination of 4.5-m pigeonpea and 1.5-m cotton produced seed was similar to that from sole pigeonpea grown in a 6-m strip. These results suggest that medium-duration pigeonpea is an ideal crop for intercropping. A comprehensive review by Ahlawat et al. (1985) indicated that pigeonpea-based cropping systems are always superior to sole cropping in cases when pigeonpea is grown as an intercrop or sequential crop with other crop species. These benefits were attributed to

Table 1. Mean pigeonpea seed yield for different pigeonpea/cotton strip intercropping systems grown under three land-configuration systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping seasons.

	Seed yield (t ha^{-1})				
Teatment	1990/91	1991/92	1992/93	1993/94	Pooled mean
Land configuration(LC)					
Flat	0.68	1.04	0.40	0.83	0.74
Ridge and furrow(RF)	0.69	1.08	0.32	0.83	0.73
Broadbed and furrow(BBF)	0.70	1.01	0.42	0.81	0.74
SE	±0.032	±0.081	±0.051	±0.044	-
F test	NS[1]	NS	NS	NS	-
CV%	8.1	13.4	23.3	9.2	-
Cropping system (CS)					
Pigeonpea:cotton strip size[m]					
6.0:0	0.84	1.57	0.49	1.02	0.98
	(100)[3]	(100)	(100)	(100)	(100)
4.5:1.5	0.91	1.20	0.49	0.98	0.98
	(0.63)	(1.18)	(0.37)	(0.77)	(0.74)
3.0 : 3.0	0.67	0.88	0.37	0.79	0.68
	(0.42)	(0.79)	(0.25)	(0.51)	(0.49)
1.5:4.5	0.35	0.52	0.19	0.50	0.39
	(0.21)	(0.39)	(0.12)	(0.26)	(0.25)
SE	±0.042	±0.125	±0.115	±0.064	-
F test	**[2]	**	NS	**	-
CV%	10.6	20.8	52.1	13.5	-
Interaction (LCxCS)					
SE	±0.065	±0.161	±0.134	±0.097	-
F test	NS	NS	NS	NS	-
CV%	14.6	15.4	32.6	18.7	-

1 NS is not significant.

2 ** is significant at P<0.01 level.

3 Figures in parentheses indicate the "expected yield" which was calculated as:

$$Ye_{ij} = Y_{jj} \times Z_{ij}$$

where Ye_{ij} =Expected yield of species i grown in association with species j.

Y_{ii}=Actual yield of species i in sole cropping

Z_{ij}=Sown proportion of species i grown in association with species j.

improved spatial and/or temporal complementarity among the component crops in the pigeonpea-based cropping systems. In addition, intercropping pigeonpea with sorghum resulted in significant reduction in wilt incidence in pigeonpea (Natarajan et al. 1985). An insignificant interaction between cropping system and land configuration system suggests that future cropping system studies with cotton and pigeonpea can be undertaken on any of the three land-configuration systems.

Seed cotton yield response

Seed cotton yield response to land configuration or cropping system by land configuration interaction was similar to that for pigeonpea seed yield. Seed cotton yield was significantly reduced by intercropping in all four years (Table 2). Intercropping pigeonpea with cotton resulted in significant yield losses in cotton. This yield reduction in cotton was mainly related to better competitive ability of pigeonpea than cotton. This was evident by a more luxuriant growth of intercropped pigeonpea than sole pigeonpea (data not shown). Yield reduction in cotton and various associated short-duration legumes and cereals have been reported in Orissa (Padhi et al. 1993) and in West Bengal (Mandal et al. 1987), which are states of India. Seed cotton yield in sole crop varied from 1.45 t ha^{-1} in 1990/91 to 2.04 t ha^{-1}

Table 2. Mean seed cotton yields for different pigeonpea/cotton strip intercropping systems grown under three land-configuration systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping seasons.

	Seed cotton yield ($t ha^{-1}$)				
Treatment	1990/91	1991/92	1992/93	1993/94	Pooled mean
Land confifiuratipn(LC)					
Flat	078	1.20	0.83	0.55	0.84
Ridge and furrow(RF)	0.75	1.10	0.69	0.62	0.79
Broadbed and furrow(BBF)	0.80	1.11	0.88	0.59	0.85
SE	±0.026	±0.066	±0.075	±0.061	-
F test	NS[1]	NS	NS	NS	-
cv%	*5.7*	10.1	16.3	18.1	-
Cropping system(CS)					
Pigeonpea : cotton strip size[m]					
4.5:1.5	0.20	0.32	0.15	0.12	0.20
3.0 : 3.0	0.56	0.77	0.53	0.25	0.53
1.5:4.5	0.89	1.42	0.87	0.49	0.92
0 :6.0	1.45	2.04	1.65	1.46	1.65
SE	±0.073	±0.121	±0.118	±0.048	-
F test	**2	**	**	**	-
CV%	16.4	18.1	25.6	14.7	-
Interaction(LCxCS)					
SE	±0.085	±0.148	±0.153	±0.107	-
F test	NS	NS	NS	NS	-
CV%	12.0	12.5	20.8	34.3	-

1 NS is not significant.

2 **is significant at P<0.01 level.

in 1991/92. Cotton was a more productive and stable crop than pigeonpea as indicated by consistently higher yields in cotton with lower coefficient of variation values (6 to 26%) when compared with pigeonpea yields (8 to 52%). The higher coefficient of variation values for pigeonpea when compared to cotton were attributed to infestation of *Helicoverpa armigera.*

The beneficial effects of land configuration on crop yields depend upon the crop species used and the severity of waterlogging. Therefore, the crop yield response to land configuration has varied greatly (Kumar et al. 1987; Rweyemamu and Boma 1990; Gupta and Sharma 1994). In the present study, the use of the raised land configurations RF and BBF did not improve yields for any of the crops because waterlogging was not a severe constraint during any of the four years.

Total dry matter production

The total dry matter (TDM) yields were not significantly affected by either land configuration treatments or treatment interactions (Table 3) during any of the years. The TDM yields decreased significantly as the strip size of pigeonpea was reduced. Averaged over 4 years, sole pigeonpea gave the highest TDM yields (6.5 t ha^{-1}), and sole cotton gave

Table 3. Total dry matter (TDM) production for different pigeonpea/cotton strip intercropping systems grown under three land-configuation systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping seasons.

	TDM yield (t ha^{-1})				
	1990/91	1991/92	1992/93	1993/94	Pooled
Treatment					mean
land configuration(LC)					
Flat	*5.5*	6.9	5.4	6.4	6.1
Ridge and furrow(RF)	5.5	6.8	5.1	6.5	6.0
Broadbed and furrow(BBF)	5.6	6.5	5.2	6.3	5.9
SE	±0.13	±0.07	±0.10	±0.12	-
F test	NS[1]	NS	NS	NS	-
cv%	4.2	1.9	3.2	3.3	-
Cropping system(CS)					
Pigeonpea : cotton strip size [m]					
6.0:0	6.2	7.3	5.3	7.3	6.5
4.5:1.5	6.3	6.9	5.5	7.2	6.5
3.0:3.0	5.7	6.2	4.6	*5.5*	*5.5*
1.5 :4.5	5.2	6.1	4.3	4.5	5.0
0 :6.0	4.0	5.8	4.1	5.9	5.0
SE	±0.20	±0.27	±0.14	±0.29	-
F test	**2	**	**	**	-
CV%	6.4	6.8	4.6	7.7	-
Interaction(LCxCS)					
SE	±0.32	±0.41	±0.27	±0.38	-
F test	NS	NS	NS	NS	-
cv%	8.2	10.2	9.0	7.9	-

1 NS is not significant.

2 **is significant at *P* <0.01 level.

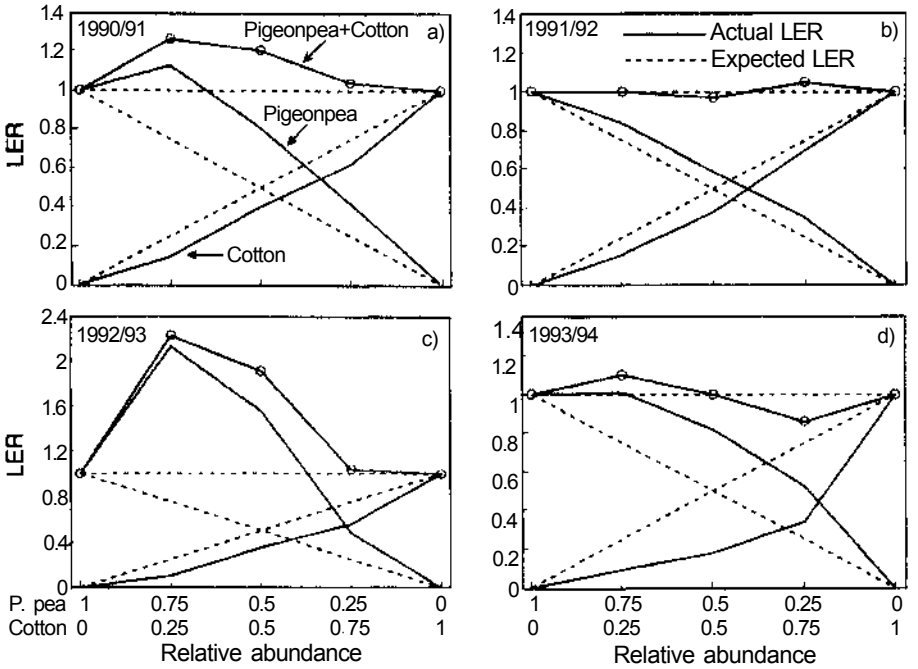

Fig. 1. Mean land equivalent ratio (LER) values for different pigeonpea/cotton strip intercropping systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping periods.

the lowest (5 t ha^{-1}). The TDM yields were generally higher in 1991/92 and 1993/94, possibly because of well distributed rainfall in these seasons.

Yield advantage of intercropping

Yield advantage of intercropping was measured by a land equivalent ratio, LER (Willey 1979) and a monetary value equivalent ratio, MVER. Mean LER values for each species and total LER values for cropping systems are presented as a replacement diagram (Fig. 1). The cropping system treatments strongly affected the mean LER values for individual species and the total LER values for cropping systems. The effects of land configuration or the interaction of land configuration and cropping system were not significant. The LER values for pigeonpea were always higher than the expected LER values in all strip intercropping combinations during the study. In contrast, cotton always gave lower than expected LER values in the corresponding strip intercropping combinations. The LER values varied from 0.35 to 2.13 for pigeonpea, and from 0.10 to 0.70 for cotton. The convex LER curves for pigeonpea and the concave LER curves for cotton indicate that pigeonpea is the most competitive species in this system. Total LER values for intercropping generally exceeded unity (Fig. 2a), indicating a yield advantage in strip intercropping. A strip combination of 4.5-m pigeonpea and 1.5-m cotton gave the highest LER value of 2.23 in 1992/93 (Fig. 2a), indicating a 123% yield advantage over either sole cropping. The observed trend in MVER values across intercropping treatments (Fig. 2b) was similar to LER trends (Fig. 2a) except

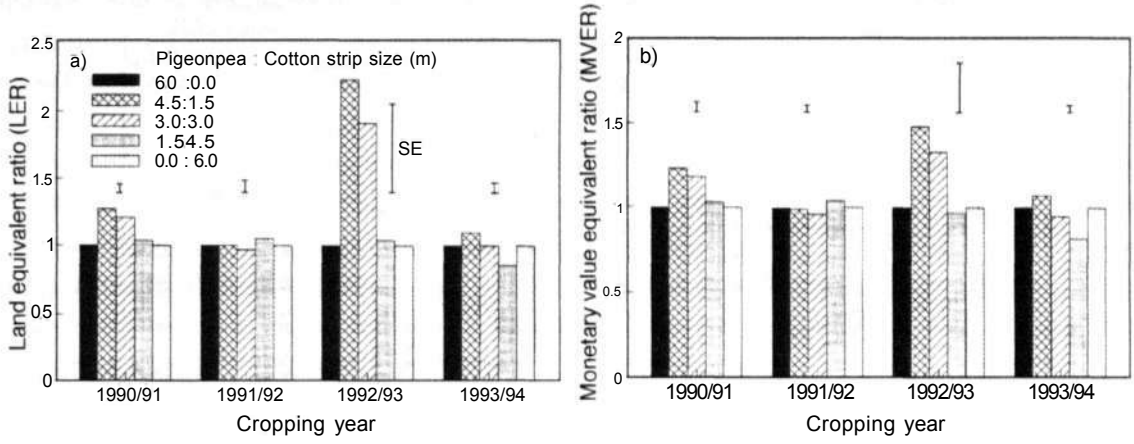

Fig. 2. Pooled land equivalent ratio (LER) and monetary equivalent ratio (MVER) values for different pigeonpea/cotton strip intercropping systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping periods.

that MVER values were generally lower than LER values. Averaged over 4 years, a strip combination of 4.5-m pigeonpea and 1.5-m cotton gave a maximum LER value of 1.4 and a maximum MVER value of 1.19. Our results are similar to studies carried out in West Bengal (Mandal et al. 1987) and in Orissa (Padhi et al. 1993) states of India, using other short-duration legumes (greengram, blackgram, peanut, soybean) and cereals (finger millet, rice) grown in intercropping systems with cottton.

Yield advantages in intercropping can be maximized by improving the degree of 'complementarity' between crop components and by minimizing inter-crop competition (Willey 1979). In the present study, there was strong inter-crop competition (Fig. 1). To maximize biological efficiency of this system, use of compatible genotypes would be required. In intercropping, temporal complementarity is more important than spatial complementarity (Willey 1979). Therefore, the component crops should have large maturity differences so as to have better temporal use of resources. In the present study, the maturity difference between pigeonpea and cotton was only about 10 days. Baker and Yusuf (1976) have quantified that there should be at least a 30- to 40-day maturity difference in component crops to capture the advantages of intercropping.

Monetary advantages of intercropping

During all four years, data on cash and labor inputs used in each cropping systems were recorded. Total cost of production for each cropping system was estimated based on the input used and the current market prices. Gross economic returns for each cropping system were estimated based on actual crop yields (stem and grain or seed cotton) and the annual average commodity prices from the primary markets in Andhra Pradesh. The total

Table 4. Total gross economic returns for different pigonpea/cotton strip intercropping systems grown under three land-configuration systems on a Vertisol at 1CR1SAT Asia Center during the 1990 to 1994 cropping seasons.

	Gross economic returns (Rs.'000ha^{-1})				
Treatment	1990/91	1991/92	1992/93	1993/94	Pooled mean
Land configuration(LC).					
Flat	9.52	18.62	12.67	14.94	13.94
Ridge and furrow(RF)	9.40	18.00	1138	15.31	13.52
Broadbed and furrow (BBF)	9.45	17.14	12.43	14.75	13.44
SE	±0.199	±0.426	±0.436	±0.399	-
Ftest	NS[1]	NS	NS	NS	-
CV%	3.6	4.1	6.2	4.6	-
Cropping system(CS)					
Pigeonpea : cotton strip size[m]					
6.0:0	7.51	16.82	6.07	12.41	10.70
4.5:1.5	9.82	17.11	7.78	13.53	12.06
3.0:3.0	10.98	19.34	10.52	12.80	13.41
1.5:4.5	11.38	23.74	12.49	12.63	15.04
0 :6.0	13.29	26.37	19.15	20.66	19.87
SE	±0.537	±1.303	±1.168	±1.054	-
F test	**[2]	**	**	**	-
CV%	9.8	12.6	16.6	12.2	-
Interaction(LCxCS)					
SE	±0.707	±1.633	±1.478	±1.457	-
F test	NS	NS	NS	NS	-
CV%	9.8	11.2	14.7	13.9	-

1 NS = Not significant.
2 ** = Significant at *P* <0.01 level.

Table 5. Total net economic returns for different pigeonpea/cotton strip intercropping systems grown under three land-configuration systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping seasons.

	Net economic returns (Rs.'OOOha[1])				
Treatment	1990/91	1991/92	1992/93	1993/94	Pooled mean
Land configuration(LC)					
Flat	6.44	14.42	7.93	10.35	9.79
Ridge and furrow(RF)	6.23	13.70	6.53	10.51	9.24
Broadbed and furrow(BBF)	6.48	12.84	7.58	9.95	9.21
SE	±0.199	±0.426	±0.436	±0399	-
F test	NS[1]	NS	NS	NS	-
CV%	5.4	5.4	10.3	6.7	-
Cropping system(CS)					
Pigeonpea : cotton strip size[m]					
6.0:0	5.09	13.32	1.87	8.69	7.24
4.5:1.5	6.99	13.13	2.90	9.25	8.07
3.0:3.0	7.71	14.84	4.97	7.99	8.88
1.5:4.5	7.59	18.73	6.26	7.29	9.97
0 :6.0	9.15	20.82	12.25	14.80	14.25
SE	±0.536	±1303	±1.168	±1.054	-
F test	**[2]	**	**	**	-
CV%	14.6	16.5	27.5	17.8	-
Interaction(LCxCS)					
SE	±0.707	±1.633	±1.478	±1.457	-
F test	NS	NS	NS	NS	-
CV%	14.6	14.6	24.4	20.3	-

1 NS is not significant.
2 ** is significant at P <0.01 level.

production cost for sole pigeonpea grown on a flat land configuration varied from Rs. 2377 ha^{-1} in 1990/91 to Rs. 4138 ha^{-1} in 1992/93. The total production costs for sole cotton grown on a flat land form ranged from Rs. 4097 in 1990/91 to Rs. 6840 ha^{-1} in 1992/93. An average additional cost of Rs. 85 ha^{-1} was required for making both RF and BBF land forms for each species. The higher total production cost in sole cotton was mainly due to additional cost involved in seed, manual planting, plant protection, and cotton picking. Total production cost for different intercropping species varied proportionally with strip size.

Total gross and net economic returns (Tables 4 and 5) were not significantly influenced by land configuration or the interaction between land configuration and cropping system over the four years. However, total gross and net economic returns responded significantly to cropping system treatments. Sole cotton always gave higher gross and net returns when compared to sole pigeonpea or any pigeonpea/cotton strip intercropping system. A strip combination of 1.5 m pigeonpea and 4.5 m cotton system was as profitable as the sole cotton system in 1990/91 and 1991/92. Gross and net economic returns increased as the strip size of cotton increased. Economic returns were higher in 1991/92 and 1993/94 because of higher yields from both species when compared to other years. Averaged over 4 years, sole cotton gave the highest gross return (Rs. 19.87 thousands ha^{-1}) and net return (Rs. 14.25 thousands ha^{-1}). The lowest gross return (Rs. 10.7 thousands ha^{-1}) and net return

Table 6. Benefit : Cost(BC) ratio values for different pigeonpea/cotton strip intercropping systems grown under three land-configuration systems on a Vertisol at ICRISAT Asia Center during the 1990 to 1994 cropping seasons.

	Benefit: Cost ratio				
Treatment	1990/91	1991/92	1992/93	1993/94	Pooled mean
Land configuration(LC)					
Flat	2.10	3.43	1.70	2.27	2.38
Ridge and furrow(RF)	1.96	3.19	1.40	2.20	2.19
Broadbed and furrow(BBF)	2.05	2.98	1.57	2.08	2.17
SE	±0.067	±0.096	±0.084	±0.078	-
F test	NS[1]	NS	NS	NS	-
CV%	5.7	5,2	9.3	6.2	-
Cropping systemtCS)					
Pigeonpea : cotton strip size[m]					
6.0:0	2.10	3.81	0.45	2.34	2.18
4.5 : 1.5	2.47	3.30	0.59	2.16	2.13
3.0:3.0	2.36	3.30	0.90	1.66	2.06
1.5:4.5	2.05	3.73	1.01	1.37	2.04
0 :6.0	2.21	3.76	1.78	2.53	2.57
SE	±0.177	±0.319	±0.228	±0.225	-
F test	NS	NS	..2	**	-
CV%	15.0	17.2	25.4	17.8	-
Interaction(LCxCS)					
SE	±0.229	±0.395	±0.288	±0.303	-
F test	NS	NS	NS	NS	-
CV%	14.3	14.9	22.4	19.4	-

1 NS is not significant.

2 **is significant at P <0.01 level

(Rs. 7.24 thousands ha^{-1}) were obtained by sole pigeonpea.

The benefit:cost (BC) ratio values varied significantly among cropping systems (Table 6), but not among land configurations or treatment interactions. The BC ratio values varied widely among cropping systems and between years (1.78 - 3.76 for sole cotton, 0.45 - 3.81 for sole pigeonpea, and 0.59 - 3.73 for strip intercropping). Higher BC ratio values for sole cotton suggest sole cotton as the most remunerative cropping system when compared with sole pigeonpea or pi geonpea/cotton strip intercropping. Averaged over 4 years, sole cotton gave the maximum BC ratio of 2.57, with the lowest BC ratio (2.04) obtained by a strip combination of 1.5-m pigeonpea and 4.5-m cotton. Sole pigeonpea gave a BC ratio of 2.18. These positive BC ratio values suggest that all cropping systems were profitable on Vertisols under rainfed conditions.

Monetary advantages of intercropping rotations

The net economic returns and BC ratio values for each 2-year sole cropping or strip intercropping rotations are given in Table 7. Strip intercropping rotations differed significantly for net economic returns and BC ratio values in both rotation cycles. However, the net returns and BC ratio values for different rotation treatments were substantially higher in the first rotation cycle (1990/1991) than in the second cycle (1992/1993). The BC ratio values for strip intercropping rotations varied significantly only in the second rotation cycle. Averaged over 2 rotation cycles, sole pigeonpea - sole cotton or sole cotton - sole pigeonepa rotation gave maximum net returns (Rs. >21 thousands ha^{-1}) and maximum BC ratio of 2.46.

Table 7. Total net economic returns and benefit : cost (BC) ratio values for different pigeonpea/cotton strip intercropping systems rotation on a Vertisol at 1CRISAT Asia Center during the 1990 to 1994 cropping seasons.

	Net economic returns (Rs.'000 ha^{-1})			Benefit: cost (BC) ratio		
Strip intecropping rotation	Cycle 1 1990 to 92	Cycle 2 1992 to 94	Mean	Cycle 1 1990 to 92	Cycle 2 1992 to 94	Mean
Strip sizes(m)						
6 pp[1] - 6 Cot[1]	25.91	16.67	21.29	3.25	1.66	2.46
4.5 pp /1.5 Cot-4.5 Cot/1.5pp	25.70	10.19	17.95	3.27	1.00	2.14
3 pp/3 Cot-3 Cot/3 pp	22.55	12.96	17.76	2.90	1.25	2.08
1.5 pp/4.5Cot-1.5 Cot/4.5 pp	20.72	15.51	18.12	2.70	1.48	2.09
6 Cot - 6 pp	22.48	20.94	21.71	2.94	1.97	2.46
SE	1.50	1.77	-	0.198	0.185	
F test	*[2]	**[2]	-	NS[3]	*	-
CV%	12.9	17.4	-	12.7	17.1	-

1 PP is pigeonpea and Cot is cotton.

2 *, ** is significant at *P* <0.05 and 0.01 level respectively.

3 NS is not significant.

Conclusion

The results from this 4-year field study indicate that pigeonpea/cotton strip intercropping is a potential system for Vertisols in the Indian SAT. Total LER and MVER values for intercropping generally exceeded unity, indicating a better biological efficiency of strip intercropping when compared with either species as sole crop. A strip combination of 4.5-m pigeonpea and 1.5-m cotton gave a maximum mean total LER value of 1.4, indicating a 40% yield advantage over a sole cotton or sole pigeonpea system. Cotton proved to be a more stable and higher yielding crop than pigeonpea. Intercropping pigeonpea had a better yield than cotton, suggesting that medium-duration pigeonpea is an ideal crop for improving complementarity in intercropping. However, pigeonpea was a more competitive crop than cotton and depressed cotton yields significantly when they were intercropped. In contrast, economic analysis indicated that sole cotton was more remunerative than sole pigeonpea or all strip intercropping combinations, and that sole pigeonpea was always inferior to strip intercropping. Results of the combined analysis of each 2-year rotation cycle showed that sole pigeonpea - sole cotton or sole cotton - sole pigeonepa rotation was the most remunerative system when compared with the other strip intercropping rotations. However, from the food security point of view and by considering the additional benefits of intercropping farmers should opt for strip intercropping rotations under low input situations and for sole crop rotations under high input situations. For increasing pigeonpea or cotton yields or monetary returns under Indian SAT conditions, use of different land configuration systems (RF or BBF) was not advantageous over the graded flat system. Future strip intercropping studies should compare the performance of crop genotypes with wider crop maturity durations.

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Above-Ground and Below-Ground Interactions in Intercropping

R. W. Snaydon[1]

Abstract

The many studies that have been carried out to compare the relative effects of shoot and root competition are reviewed, giving special attention to the validity of the experimental methods used.

The yield advantage of intercropping, as measured using land equivalent ratio (LER), was usually greater when components shared only aerial resources, i.e., light, than when they shared only soil resources, i.e., mineral nutrients and water. Similarly, resource complementarity, as measured by relative yield total (RYT), was greater when components shared only aerial resources. Conversely, the severity of competition experienced by components was greater when components shared only soil resources. These results indicate that mixture components usually compete more intensely for soil resources than for light.

Differences between components in root competitive ability were generally greater than differences in shoot competitive ability. This partially reflects the fact that competition was usually greater for soil resources.

The experimental techniques used in competition studies have generally been inadequate to define the particular soil resources for which competition occurred, though nitrogen and water have been implicated in many studies. Similarly, the techniques used in intercropping studies have usually been inadequate to define the nature of intercropping advantage. However, mixtures of legumes and non-legumes have usually given the largest intercropping advantage, and the use of different forms of nitrogen (N) by the components appears to be the main cause of that advantage.

Introduction

The historical development and use of intercropping systems has been pragmatic and empirical, i.e., based on experience rather than theory. Until recently, intercropping systems have been based solely upon the experience of farmers, with few of the possible alternatives compared, inadequate measurement made of crop yield and quality, and no replication of the various systems. More recently, wider ranges of species combinations, densities, and

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agronomic treatments have been compared in properly replicated experiments, with crop yields and quality measured more accurately. However, the results of these experiments have still been used mainly to make post hoc decisions on the most suitable system for the particular set of environmental and agronomic conditions used, rather than to define the ecological basis of intercropping advantage, and so to determine ways of predicting the best crop combinations for particular conditions.

The possible mechanisms by which intercrops may outyield their corresponding monocultures are classified in Table 1. Only one of these mechanisms does not involve some aspect of competition between the components. The exception is mechanism Ia, where one component "protects" the other from pest or pathogen attack by being either a barrier to spreading or, perhaps, by being a deterrent. In the other mechanism involving pests and pathogens (Ib), the yield and competitive ability of the susceptible component are reduced when attacked, but the resistant component then gains a greater share of limiting resources, and the yield of the mixture is reduced less than the means of the monocultures.

In mechanism 2, each *individual* mixture shows no yield advantage over its corresponding monocultures, but there is an overall advantage when yields are averaged across all sites or years, provided the more competitive component is also the higher yielding component in each environment (Snaydon & Harris 1981). Conversely, if the more competitive component is the lower yielding component, intercrops would show a disadvantage, when yield is averaged across all sites or years. This mechanism has received surprisingly little attention, though the related question of the yield stability of mixtures has received some attention.

Mechanisms involving partial competition (mechanism 3) have received the most attention in studies of intercropping. In particular, the use of partially different resources in time or space (mechanism 3b), and the use of different forms of a given resource (mechanism 3ai) have attracted considerable attention. By contrast, the possibility that different resources may limit the two components of a mixture (mechanism 3aii) has rarely been considered.

Table 1. Classification of the mechanisms that may give rise to intercropping advantage.

1. Components compete fully but the effects of pests or pathogens are reduced:
   - (a) component I "protects" component J
   - (b) component I replaces component J
2. Components compete fully but respond differently to environmental variation:
   - (a) in space
   - (b) in time

   This mechanism gives no intercropping advantage in any single environment, but advantages may occur if yields are summed across several environments (see text)
3. Components only partially compete:
   - (a) different limiting resources
     - (i) different form of resource (e.g., N_2 & NO_3)
     - (ii) different resources limiting
   - (b) same limiting resource but partially different use:
     - (i) in time
     - (ii) in space

Because most mechanisms of intercropping advantage involve aspects of competition, a fuller understanding of intercropping depends on a fuller understanding of the nature of competition between intercrop components. The limiting resources for which components compete must first be identified, then the mechanisms by which intercrops use limiting resources more efficiently must be defined, since this largely determines intercropping advantage. The relative abilities of the components to compete for limiting resources must also be measured, and the factors that affect it defined, because this determines the composition of mixtures, and hence the nutritional and economic value of the harvested crop. Such information should allow more accurate predictions of suitable combinations of crops, and the agronomic conditions that favor particular combinations.

An important first step in understanding the nature of competition between components in intercrops is to separate the effects of shoot competition and root competition. The distinction is important because of differences in the nature and availability of resources above-ground and below-ground, and because of differences in the morphology and physiology of shoots and roots. Wilson (1988a) has already reviewed many studies comparing shoot and root competition; this review updates his study, giving particular attention to intercrops and to the relation between the experimental methods used and the results obtained, it also briefly considers the specific resources for which components compete. The main objectives of the review are (1) to critically evaluate the techniques that have been used to compare shoot and root competition, (2) to review the results of previous comparisons of shoot and root competition, and (3) to briefly consider the methods used for defining the resources for which components compete.

Evaluation of methods

Studies of intercrops are inherently more difficult than those of single crops, because of the reciprocal effects between components. In intercrops, each component both affects and is affected by the other component(s), so that the experimental designs and the methods of data analysis for studies of intercrops are very different from those used in studies of individual crops.

Data analysis

The basic problem with analyzing the data from intercropping studies is that the performance of the two components must be considered simultaneously. The nature of this problem, and its solution, is most easily seen by reference to the simplest type of mixtures, i.e., binary mixtures.

The yields of the two components in any binary mixture, together with the yields of the corresponding monocultures, can be effectively presented by plotting the yield of one component against that of the other (Pearce & Gilliver 1979). Such bivariate diagrams are more effective if the relative yield (RY_i) of component I, i.e., the ratio of its yield per unit area in mixture to that in monoculture (Y_{ij}/Y_{ii}), is plotted (Fig. Ia) against the relative yield of component J (RY_j) (Snaydon & Satorre 1989). Two new axes (ON) and (XY) can then be

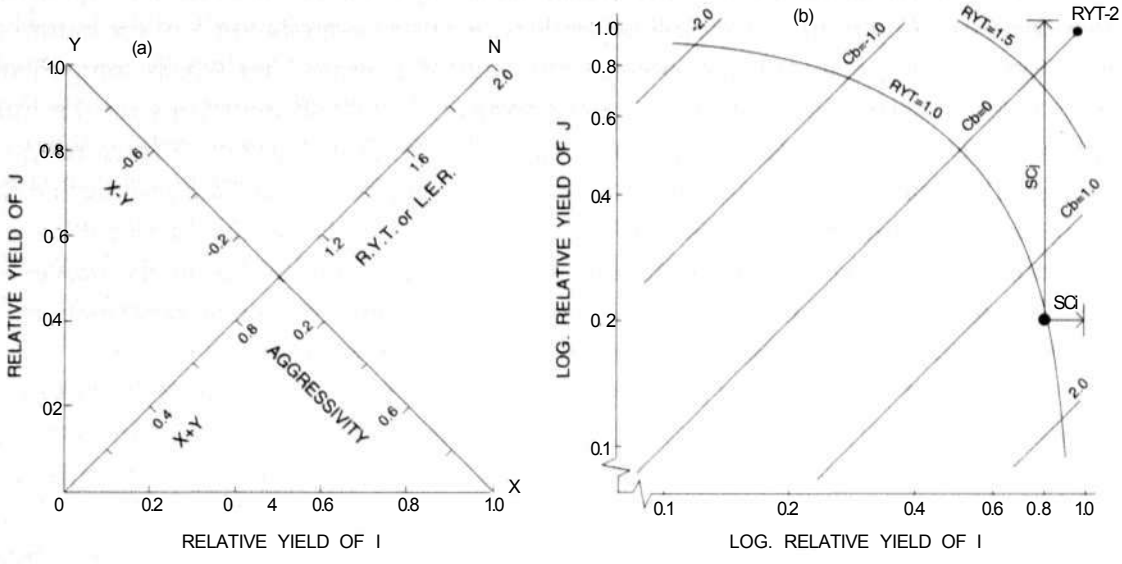

Fig. 1. (a) A bivariate diagram, based on the relative yields of components I and J in monocultures and binary mixtures, showing how values of resource complementarity (RYT) and competitive ability (aggressivity) are derived, (b) A bivariate diagram, based on logarithmic transformation of the relative yields of I and J, showing how resource complementarity (RYT), competitive ability (competitive balance index, C_b) and the severity of inter-component competition experienced by 1 (SC_i) and by J (SCj) are derived. See text for detailed explanations.

constructed at right angles to those of RY_i and RY_j. The new NE-SW axis (ON) represents the sum of RY, and RYj, while the new NW-SE axis (XY) represents the difference between RY_i and RYj (Fig. la). These two new axes are important because they measure previously accepted indices of competition. The sum of RY_j and RY_j, i.e. $Y_{ij}/Y_{ii} + Y_{ji}/Y_{jj}$, measured along the NE-SW axis, is both RYT of de Wit (1960) and LER of Mead & Willey (1980); the line joining the two monoculture yields obviously represents conditions where RYT = LER = 1.0 (Fig. la). Because LER is widely used to measure the yield advantage of intercropping, the NE-SW axis (ON) can be used to measure intercropping advantage for any given mixture. Similarly, RYT is widely accepted as a measure of the extent to which competition occurs between components, i.e., the resource complementarity that exists between them (Snaydon & Satorre, 1989), so resource complementarity can also be measured along the NE-SW axis (ON). Although LER and RYT are calculated in the same way, there are important differences between the indices; firstly, LER is usually based on grain yield, whereas RYT is usually based on total biomass; secondly, as we have seen, LER is interpreted in an agronomic context, while RYT is interpreted in an ecological context.

The new NW-SE axis (XY) of a bivariate diagram based on relative yields (Fig. la) measures the difference between the relative yields of I and J (RY_i & RY_j), i.e., $Y_{ij}/Y_{ii} - Y_{ji}/Y_{jj}$. This index, termed "aggressivity" by McGilchrist & Trenbath (1971), has been widely used as a measure of the relative competitive abilities of the components, so competitive ability can be measured along the NW-SE axis (XY). However, because lines of equal aggressivity run parallel to the new NE-SW axis (ON), whereas lines of equal competitive ability radiate out from the origin (Snaydon & Satorre, 1989), ''aggressivity" is an imperfect measure of

competitive ability. This problem can be overcome (Snaydon & Satorre 1989) by plotting the logarithm of relative yields in the bivariate diagram (Fig. Ib). Axis XY then becomes $\log_e (Y_{ij}/Y_{ii} \div Y_{ji}/Y_{jj})$, which is the "competitive balance" index (C_b) of Wilson (1988a), and also the log. transformation of the "competitive ratio" of Willey & Rao (1980); both of these indices are recognized measures of competitive ability. Lines of equal values of these indices run parallel in the NE-SW diagonal (Fig. Ib), and the scale is linear. There is, however, a slight disadvantage in using logarithmic transformation of relative yields, i.e., that the lines of equal RYT/LER values are now curved (Fig. Ib), though they run parallel to each other.

Because measures along axes XY and ON are mathematically independent of one another, the two resulting indices of competition, i.e., resource complementarity and competitive ability, are *mathematically* independent of one another. However, although the two indices of competition are mathematically independent of one another, there are biological factors that cause them to be partially related. In particular, in the absence of any stimulatory effect of one component on another, each component will not yield more in mixture than it does in monoculture, i.e., relative yield values of the components will not exceed 1.0. As a result, all values lie within the triangle YNX (Fig. Ia), and values of competitive ability will decrease as RYT values increase above 1.0, reaching zero at RYT 2.0. This is logical, because the competitive advantage or disadvantage of components will decline as competition between them declines, and neither component will have a competitive advantage over the other if the two components do not compete.

A third index of competition, the severity of inter-component competition experienced by each component (Snaydon & Satorre 1989) can also be measured, using the bivariate diagram, and its relation to the two other indices can be demonstrated. The severity of inter-component competition experienced by each component in a mixture is measured as the logarithm of the ratio of the yield per unit area of a component in monoculture (Y_{ii}) to that in the relevant mixture (Y_{ij}), i.e., $\log_e (Y_{ii}/Y_{ij})$, which is the logarithm of the inverse of relative yield (see above); this has been termed the relative severity of competition by Snaydon (1991a). Valid measurements of the severity of inter-component competition can only be made if an additive design is used; in replacement designs, the density of the components is different in mixtures and monocultures, and inter-component competition is confounded with intra-component competition (Snaydon 1991a). The severity of inter-component competition experienced by component I is measured along axis X of the bivariate diagram of logarithm of the relative yield (Fig. Ib), while that of component J is measured along axis Y. It is therefore apparent that the severity of inter-component competition experienced by each component is affected both by the degree of resource complementarity between components and by the relative competitive abilities of the components.

Experimental designs

Replacement designs, in which mixtures are formed by substituting a given number of plants of one component by an equal number of those of the other component, have been used extensively for studies of intercropping and plant competition, but have been subject

to increasing criticism for two decades. Replacement designs give values of resource complementarity and competitive ability that are difficult to interpret, because values of those indices are affected by the density of the monocultures, the shape of yield-density response curve of the monocultures, and the proportions of the components in the mixture (Snaydon, 1991a). In addition, replacement designs cannot be used to obtain values of the severity of competition (see above). By contrast, additive designs, in which mixtures are formed by adding plants of one component to those of the other, give values of resource complementarity, competitive ability, and severity of competition that are more easily interpreted (Snaydon 1991a). If the objective of an intercropping study is to find the optimum mixture, however, neither simple replacement designs nor simple additive designs are adequate. The optimum mixture is likely to have a density that is higher than that of a replacement design, regardless of whether the monocultures are grown at identical densities or each at the optimum density. However, the optimum mixture is also likely to have a density that is lower than an additive mixture based on monocultures at their optimum densities (Willey 1979). The optimum combination can only be found by varying the densities of the components independently, preferably in a bivariate factorial design, i.e., a type of additive design (Snaydon 1991a).

Separating shoot and root Interactions

The effects of shoot competition and root competition can be separated by using above-ground and below-ground partitions. Unfortunately, the partitions also affect plant performance, so the partitions must be present in all treatments, so that extraneous effects are consistent across all treatments. If the relative effects of shoot and root competition are to be assessed, both above-ground and below-ground partitions must be used; this also allows any interactions between shoot and root competition to be measured. The design should be additive (see above), and the performance of both components should be measured, so that indices of resource complementarity and competitive ability can be calculated. Remarkably few studies satisfy all these requirements (Table 2).

Many studies comparing shoot and root competition have only used partitions in some treatments (Table 2b & d), so confounding the effects of the form of competition with the effects of the partitions per se. If monocultures are also grown both with and without partitions (Table 2d), the problem is partially overcome, but a more satisfactory approach is to use density as an additional experimental variable (e.g. Snaydon & Howe, 1986).

A number of studies that claim to have separated the effects of shoot and root competition (e.g., Chamblee 1958; Assemat et al. 1981; Willey & Reddy 1981; Regnier et al. 1989; Perera et al. 1992) have only investigated the effects of root partitions, so giving data on no competition, shoot competition only, and full competition (both root and shoot). Estimates of the effects of root competition might then be obtained by the differences, provided no interaction occurred between shoot and root competition. However, because both positive and negative interactions can occur between shoot and root competition (Wilson, 1988a), these studies are of dubious value, and are not considered here.

Some other comparisons of shoot and root competition are suspect because the methods of eliminating shoot competition are suspect. For example, Cook & Ratcliffe (1984,

Table 2. Details of the experimental methods used in various studies that have compared the effects of shoot and root interactions, and a compilation of the results obtained.

Reference[1]	L/R[2]	M.C.[3]	Oth.Tr.[4]	Res.Comp.[5] S R =	Cpt.Abil.[6] S R =	Sev.Comp.[7] I J S R =	Sp.[8] S R =	
(a) Additive experiments, partitions always present								
D. ('58)	Rad.	2	2N	2 0 0	0 2 0	0 0 2	0 2 0	GG
S. ('67)	Lin.	2	2Ss	0 1 1 1	1 0(O)	1 1 0	1 0 1	LH
K. ('71)	Rad.	2	2Nx2P(x3Sd)	4 0 0	0 2 2(O)	0 4 0	0 4 0	*GG*
G&W. (75)	Rad.	2	21n	0 1 1 2	0 0	0 2 0	0 2 0	LH
E&B. (75)	Lin.	2	3Sp	1 0 2	0 2 1(O)	0 0 3	0 2 1	HG
G&V. ('88)	Rad.	2		1 0 0	0 1 0	1 0 0	1 0 0	GL
B&O. ('90)	Rad.	2		1 0 0	0 0 1	0 1 0	0 1 0	LH
E&S. ('92)	Lin.	2	2N(x4D)	0 0 2	1 1 0	0 0 2	2 0 0	CG
E&S. ('92)	Lin.	2	4Sd(x2Sd)	4 0 0	0 4 0	0 4 0	0 4 0	CG
S&S. ('92)	Lin.	2	3Spx2Cv(x2N)	6 0 0	0 6 0	0 5 1	0 6 0	GC
T,P&S('93)	Lin.	2	2Spx2Cvx3Sd	6 0 0	0 6 0	0 0 6	0 6 0	CL
Number of cases				25 2 6	4 25 4	2 17 14	4 27 2	
(b) Additive experiments, partitions sometimes present								
C&R. ('84)	N	1	2F(x3Td)	NA	NA	0 2 0	NA	GG
C&R. ('85)	N	1	2Spx2F	NA	NA	0 4 0	NA	GLG
S&H. ('86)	N	1	3Spx3F(x4D)	NA	NA	0 9 0	NA	GG
J&N. ('90)	N	1	3F	NA	NA	0 3 0	NA	HG
S,K&C('92)	N	1		NA	NA	0 1 0	NA	GG
Number of cases				NA	NA	0 19 0	NA	
(c) Replacement experiments, partitions always present								
S. (71)	Rad.	2	2Cvx2So	1 1 2	2 2 0	NA	NA	LL
L&I. (74)	Lin.	2		0 0 1	0 1 0	NA	NA	HH
R&S. ('80)	Lin.	2	2F	0 0 2	0 2 0	NA	NA	GG
M&S. ('82)	Lin.	2	2N(x2D)	0 0 2	0 1 1	NA	NA	CL
M&S. ('82)	Lin.	2	2Nx2Sd	0 4 0	0 4 0	NA	NA	GG
S&B. ('82)	Rad.	2	2H	0 0 2	0 1 1 (O)	NA	NA	GG
M&F. ('84)	Lin.	2	2N	0 0 4	2 0 2	NA	NA	GL
M&F. ('88)	Lin.	2	3Sd	0 0 3	0 3 0	NA	NA	CG
S&S. ('89)	Lin.	2	2N(x4Sp)	0 2 0	0 2 0	NA	NA	CG
Number of cases				1 716	4 16 4			
(d) Replacement designs, partitions sometimes present								
W&G. ('64)	N	2	4Sw	0 3 1	3 0 1	NA	NA	GL
R. ('68)	Lin.	2	2Spx2D	1 0 3	1 2 1	NA	NA	GG
E. (72)	Lin.[9]	2	2TeDa	1 1 0	0 2 0	NA	NA	GG
S&L. ('80)	Lin.	2	2So	0 1 1	0 2 0	NA	NA	GL
W&N. ('87)	Lin.	2	2F	0 2 0	0 2 0	NA	NA	*GG*
A,B&A('91)	Lin.[9]	2	3Spx2F	3 3 0	1 2 3	NA	NA	HH
Number of cases				5 10 5	5 10 5			

1 Author(s): initial letter(s) and date.

2 Arrangement: radial (Rad.), linear (Lin.) or neither (N).

3 Measured components: one (1) or both (2).

4 Other treatments: nitrogen (N), seed size (Ss), phosphate (P), infection (In), species (Sp), density (D), sowing date (Sd), fertilizer (F), cultivar (Cv), tube diameter (Td), soil (So), soil water (Sw), temperature (Te), daylength (Da). Treatments in brackets not considered.

5 Number of cases where resource complementarity (RYT) was greater with root than shoot competition (R), RYT greater with shoot than root competition (S), or no difference (=).

6 Number of cases where the root competitive ability of the more competitive component was greater than the shoot competitive ability (R), shoot competitive ability greater than root competitive ability (S), or no difference (=), (0) indicates cases where one component had the greater root competitive ability but the other component had greater shoot competitive ability. Competitive ability measured as C_b (Wilson 1988).

7 The number of cases where the severity of shoot competition experienced by a component (I or J) was greater than the severity of root competition (S), severity of root competition greater than shoot (R), or no difference (=).

8 Species used: grass (G), cereal (C), legume (L), non-leguminous herb (H).

1985), Jeangros & Nosberger (1990), and Seager et al. (1992) all used defoliation to eliminate shoot competition (Table 2b) but, because defoliation also reduces root competition in some species (Remison & Snaydon 1980), defoliation is likely to exaggerate the effects of shoot competition. The use of wire screens (e.g., Cook & Ratcliffe 1985) and transparent above-ground partitions (e.g., Wilkinson & Gross 1964; Rhodes 1968; Scott & Lowther 1980; Brede & Duich 1986) is also somewhat suspect.

Many studies of the comparative effects of shoot and root competition have used replacement designs (Table 2c & d), so that the resulting data are difficult to interpret (see above). It gives me no pleasure to note that I have proposed replacement designs as alternatives to the two additive designs that have formed the basis of most comparisons of shoot and root competition, i.e., the radial design of Donald (1958) (see Snaydon 1971) and the linear design of Schreiber (1967) (see Snaydon 1979). In some studies (e.g., Cook & Ratcliffe 1984 & 1985; Snaydon & Howe 1986; Jeangros & Nosberger 1990; Seager et al. 1992), only data for one component are presented (Table 2b), so that resource complementarity and competitive ability cannot be calculated, though the severity of inter-component competition experienced by the measured component can be calculated, because additive designs were used in each case.

Although these various design faults prevent valid comparisons of the effects of shoot and root competition in many studies, the results from those studies do provide an opportunity to assess the effects of experimental methods on the results obtained.

Relative effects of shoot and root competition

The relative effects of shoot and root competition in intercropping can be measured in terms of: (1) yield advantage, (2) resource complementarity, (3) competitive ability and (4) the severity of competition experienced by each of the components. Wilson (1988a) recognized these four effects, though the measure of severity of competition that he used, i.e., the competitive intensity index, is invalid (Snaydon 1991a), and his measure of yield advantage, i.e., the relative yield of the mixture, is of little agronomic value. We have already seen that the most commonly used measure of yield advantage in intercropping, LER, is calculated in the same way as the most commonly used measure of resource complementarity, i.e., RYT. Measures of competitive ability are important, because competitive ability determines the relative abundance of the components in intercrops, and therefore affects the economic and nutritional value of the harvested crop. Measures of the severity of competition have no direct agronomic significance, but may help clarify the nature of competition between components.

In this study, yield advantage is measured by LER, which is identical to RYT, the usual measure of resource complementarity (see above); competitive ability is measured by the competitive balance index (C_b) of Wilson (1988a), whereas the severity of inter-component competition experienced by each component is measured by $\log_e Y_{ii}/Y_{ij}$ (see above). An analysis of variance was carried out on the values of each of these indices, obtained from the various species and treatment combinations in each study where an additive design was used and where both components were measured (Table 2a). The various

"experimental conditions", i.e., experiments and "other treatments" (Table 2), were used effectively as replicates, and the "form of competition" mean square was tested against the "form of competition x experimental conditions" mean square; this form of analysis tests how consistent the differences between forms of competition are, across various environmental conditions. No analyses of variance were carried out on replacement designs, except for yield advantage, because of difficulties in interpreting the indices (see above).

Yield advantage

The use of LER as an agronomic measure of yield advantage is valid, whether or not an additive or a replacement design is used, though neither the additive nor replacement designs used are likely to have provided the optimum mixture density (see above). It should also be recognized that most of the values of LER/RYT presented here are based on biomass production, rather than grain yield; however, where values have been based on both measures (e.g., Tofinga et al. 1993), the results have been similar.

In additive experiments (Table 3), the mean LER value, which is the same as the RYT value (see above), was significantly greater ($P < 0.001$) when only the shoot systems of the components interacted (1.50) than when only the root systems interacted (1.27) and was least (1.19) when both shoot and root systems interacted. The equivalent mean LER (or RYT) values for replacement experiments were 0.98 when only shoot systems interacted, 1.06 when only root systems interacted, and 1.03 when both shoot and root systems interacted (Table 3), with no significant difference ($P > 0.05$) between these values. These results, based on a large number of studies in a wide range of conditions, indicate that additive mixtures normally gave greater yield advantages than did replacement mixtures ($P < 0.001$), whether the components shared aerial resources, soil resources, or both. The higher LER values in additive mixtures, compared with replacement mixtures, probably resulted from the fact that the overall density of an additive mixture is twice that of a corresponding replacement mixture; Willey (1979) concluded that the optimum density for an intercrop is usually greater than that of a replacement mixture based on monocultures grown at their optimum densities. However, the density of an additive mixture based on optimum monoculture densities is likely to be supra-optimal.

Table 3. Mean values for resource complementarity (RYT), which are also LER values, and for competitive ability (C_b) for three types of experimental design, in which only the shoots of components interacted (S), only the roots interacted (R) or both the shoots and roots interacted (RS). See Table 2 for a listing of the various studies summarized here. n = number of observations.

	Res, Complementarity				Competit. ability		
Experimental design	n	S	R	SR	S	R	SR
Additive, partitions always present	24	1.50	1.27	1.19	0.48	0.67	1.05
Replacement, partitions always present	18	0.98	1.06	1.03	0.17	0.39	0.60
Replacement, partitions sometimes present	17	1.08	1.18	1.08	0.39	0.58	1.21

Resource complementarity

Although RYT values are commonly used to define resource complementarity, valid interpretation is only possible where additive designs have been used (Snaydon, 1991a). In additive experiments, RYT values of 2.0 indicate that there is no competition between components, i.e., complete resource complementarity, whereas RYT values of 1.0 indicate complete competition between components, i.e., no resource complementarity (Snaydon 1991a).

We have already seen (Table 3) that, in additive experiments, the mean RYT/LER value when components shared only aerial resources (1.50), was significantly greater ($P < 0.001$) than when they shared only soil resources (1.27) or shared both aerial and soil resources (1.19). In passing, it is worth noting that it is not possible to compare these mean RYT values with those obtained by Wilson (1988a) in his earlier review, because he excluded additive experiments from his survey of RYT values. Where components only shared aerial resources, in additive mixtures, RYT values ranged from 1.0 to 2.0 (Fig. 2a); in five cases they exceeded 1.9 (Donald 1958; King 1971), indicating essentially no competition between components for light. At the other extreme, there were only two cases (Evetts & Burnside 1975; Exley & Snaydon 1992) where RYT values approached 1.0, indicating almost complete competition for light. These results indicate that competition between components for light is usually only partial. Such partial competition for light could occur either because (a) the components were potentially capable of competing for light, but the combined densities of the components in the mixture were insufficient to fully utilize the light supply, so only partial competition for light occurred both within and between components, or (b) the density of each component in its monoculture was sufficiently high to cause competition for light within components, but the components did not fully share the light in either space or time (mechanism 3, Table 2). Cause (a) seems to be the most likely explanation for the generally high values of RYT observed, when components shared only aerial resources in additive mixtures (Fig. 2a), because (1) it seems unlikely that the components could have used almost totally different light supplies, in either time or space, to give RYT values close to 2.0, (2) in the only study to vary plant density (Exley & Snaydon 1992), increasing the density of the mixture reduced RYT values, (3) RYT values decreased progressively with time, as the plants used more resources, in the study by Groves & Williams (1979), (4) applications of N fertilizer, which increased dry matter production and light use, reduced RYT values (Donald 1958; Tofinga 1990; Satorre & Snaydon 1992).

When components shared only soil resources in additive mixtures, the results fell broadly into two groups (Fig. 2b). In 10 cases, values of RYT were close to 1.0, indicating complete competition for soil resources. In the other 14 cases, values of RYT were around 1.5; in 8 of those 14 cases the mixtures consisted of legumes with non-legumes, and the resource complementarity can probably be attributed to the use of different sources of N (see below). In 4 of the other cases, involving mixtures of grasses (King 1971), the high RYT values can probably be attributed to the low densities used (see above).

Where components shared both aerial and soil resources, most RYT values were between 1.0 and 1.5 (Fig. 2c). Most of the higher values were for mixtures of legumes with non-legumes, and are probably attributable to different N sources (see below); the other high values (King 1971) can probably be attributed to low densities (see above).

The results of this analysis indicates that competition for soil resources was more common, and more intense, than competition for light. However, the relative extent to which competition occurs for aerial and soil resources will obviously depend upon the conditions used in the experiment. If an infertile soil is used, or water is inadequate, soil factors are likely to be most limiting. On the other hand, if adequate nutrients and water are available, light will become the main limiting factor. Most of the studies reviewed here used agricultural soils, and additional fertilizer was often supplied, whilst the stands were usually adequately watered; in spite of this, soil factors were usually the most limiting. Soil factors are more likely to be limiting in most field situations, because mineral nutrients and water are so commonly limiting factors in agricultural situations, more especially in the low-input systems under which intercrops are normally grown. Further reasons for concluding that light is rarely a limiting resource are presented elsewhere (Snaydon 1991b). In tropical and sub-tropical areas, high radiation receipts mean that light is less likely to be limiting, while increased evapotranspiration will increase water deficits and competition

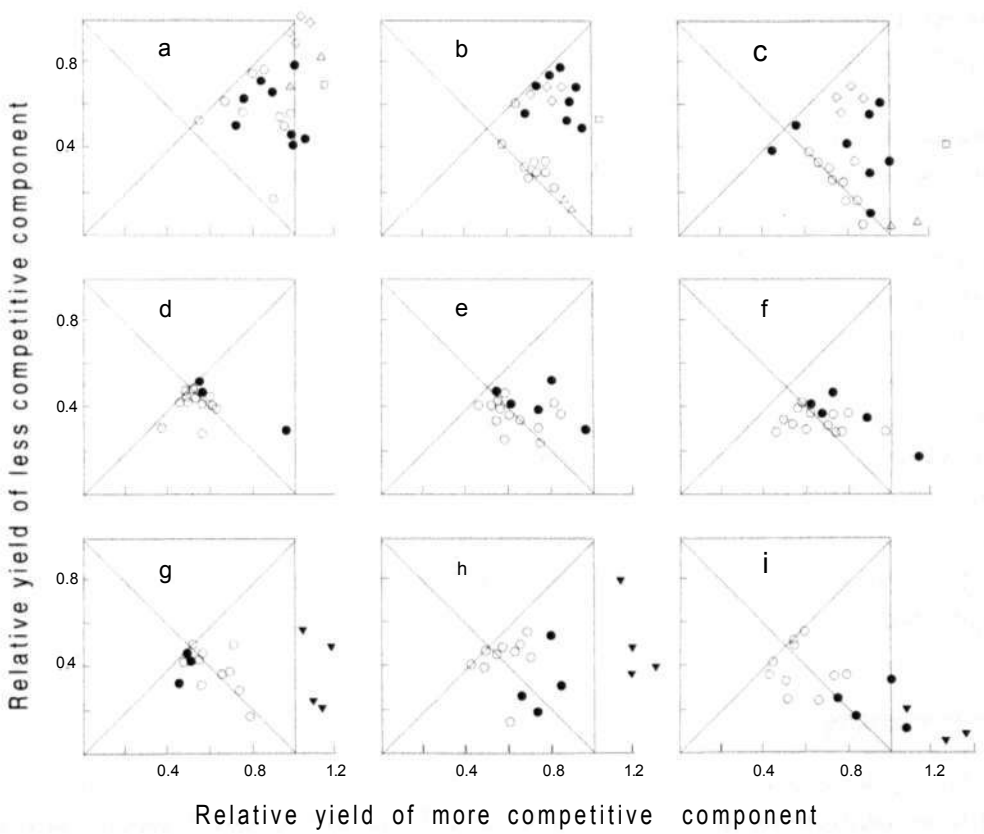

Fig. 2. Bivariate diagrams presenting the data from various studies comparing shoot and root interactions between components in mixtures. (a) - (c) Studies using additive designs with partitions always present; △ = Donald (1958), ◇ = King (1971), □ = Evett & Burnside (1975). (d) - (f) Studies using replacement designs with partitions always present. (g) - (i) Studies using replacement designs with partitions only sometimes present; ▽ = Wilkinson & Gross (1964). (a), (d) & (g) are shoot interactions only; (b), (e) & (h) are root interactions only; (c), (f) & (i) are both shoot and root interactions. Filled symbols indicate mixtures of legumes with non-legumes, open symbols indicate all other mixtures. See Table 2 for further details of the studies and the text for an interpretation of the diagrams.

for water; similarly, rapid plant growth will lead to nutrient deficiencies and more intense competition for nutrients.

In replacement experiments, the mean value for RYT was 0.98 when the components shared aerial resources, 1.06 when they shared soil resources, and 1.03 when both aerial and soil resources were shared (Table 3); the equivalent values in the review by Wilson (1988a), where half as many values were surveyed, were rather lower, i.e., 0.94, 1.00, and 0.95, but in the same sequence. These mean values, for RYT in replacement experiments, were significantly less ($P < 0.001$) than those in additive experiments, i.e., 1.50, 1.27, and 1.19, respectively. This confirms the conclusion (Snaydon 1991a), based on theoretical considerations, that replacement designs usually underestimate resource complementarity. It is worth noting that complete competition, whether for light or soil factors, is even less likely to occur in replacement mixtures than in additive mixtures, because the densities in replacement mixtures are only half those in equivalent additive mixtures.

In replacement experiments where partitions were only sometimes present, the pattern of results (Figs. 2 g-i) was generally similar to that where partitions were always present (Figs. 2 d-f); however, when partitions were only sometimes present, there were 4 values to the extreme right of each figure (Figs. 2g,h&i), i.e., the relative yield of one component was substantially greater than 1.0, regardless of the form of competition. These values are all from the study by Wilkinson & Gross (1964), and probably reflect the effects of the partitions used, rather than the effects of competition per se. In view of this and the effects of partitions, in studies where monocultures were grown both with and without partitions (Eagles 1972; Aerts et al. 1991), it would be wise to disregard the results of studies where partitions were only sometimes present.

When partitions were always present, there were few cases where components appeared to have relative yields greater than 1.0. However, Evetts & Burnside (1975) found a relative yield of 1.27 when *Sorghum bicolor* competed both above-ground and below-ground with *Asclepias syriaca* (Fig. 2c); values were also greater than 1.0 with shoot competition only (Fig. 2a) and root competition only (Fig. 2b), but none of these values was significantly greater ($P > 0.05$) than 1.0. The various studies, using different species, different environments, and different experimental design, therefore provide little evidence that the presence of one component, either above-ground or below-ground, stimulates the growth of another.

Competitive ability

In the various studies using additive designs, the mean competitive ability of the most competitive component, as measured by the C_b index of Wilson (1988a), was greater ($P 5= 0.05$) when the components competed for soil resources (0.67) than when they competed for aerial resources (0.48), and was even greater ($P.< 0.001$) when both shoot and root competition occurred (1.05) (Table 3). There were 25 cases where the components differed more in root competitive ability than in shoot competitive ability, but only 4 cases where they differed more in shoot competitive ability than root competitive ability (Table 2a). In general, therefore, components differed more, and differed more often, in root competitive ability than in shoot competitive ability. To some extent, this seems to have

been due to the fact that resource complementarity for aerial resources was greater than that for soil resources (Table 3 & Figs. 2a&b); we have already seen that as RYT approaches 2.0, i.e., conditions of no competition, the relative competitive ability of the components decreases towards zero, and this clearly happened when components shared aerial resources (Fig. 2a). However, even in cases where the components were in almost complete competition, i.e., RYT between 1.0 and 1.2, there was still some evidence that components differed more in root competitive ability (Fig. 2b) than in shoot competitive ability (Fig. 2a), though there were too few cases, especially for shoot competition, to draw any firm conclusion.

Measures of competitive ability, whether of aggressivity (McGilchrist & Trenbath 1971) or of competitive balance (C_b) (Wilson 1988a), are more difficult to interpret when replacement designs have been used (Snaydon 1991a), so the results of studies using replacement designs should be treated with caution. However, the various replacement experiments gave essentially similar results to those of additive experiments, though there were also important differences. As in the case of additive experiments, the mean C_b value when components competed only for soil resources (0.39), in replacement experiments with partitions always present (Table 3), was greater than when they competed only for aerial resources (0.17), and was greatest (0.60) when components competed for both aerial and soil resources. These results again indicate that the components generally differ more in root competitive ability than in shoot competitive ability. Notice that the mean C_b values were less in replacement experiments than in additive experiments (Table 3); this probably reflects the fact that densities were lower in replacement mixtures. The mean values of C_b for each form of competition (shoot, root, and full), in replacement experiments where partitions were only sometimes present (Table 3), generally followed the same pattern as for additive and replacement experiments where partitions were always present. However, the results from those experiments should be treated with extreme caution, because the presence of partitions is confounded with competition treatments (see above).

Wilson (1988a), using a smaller number of studies than in this review, and including both additive and replacement designs, as well as experiments with partitions only sometimes present, found a mean C_b value of 0.73 when components competed only for soil resources, 0.32 when they competed only for aerial resources, and 1.03 when they competed for both aerial and soil resources. He found more than twice as many cases where the components mainly differed in root competitive ability than where they mainly differed in shoot competitive ability. These results are essentially the same as the mean of additive and replacement experiments reviewed here. On the basis of these two reviews and regardless of the experimental methods used, therefore, it seems that species usually differ more in root competitive ability than in shoot competitive ability. It is usually assumed that differences in competitive ability between species or cultivars are attributable to shoot characteristics, such as plant height or leaf structure. However, species and cultivars also differ in root characteristics, e.g., size, distribution, and uptake efficiency, that are likely to affect competitive ability. The most likely reason why differences in root competitive ability were larger and more numerous than differences in shoot competitive ability is that competition for soil resources was generally more intense than competition for light, as indicated by RYT values in additive experiments (Table 3).

Severity of competition

The severity of competition experienced by each component in a mixture can only be measured in additive mixtures (see above). In additive experiments where both components were measured (Table 2a), the mean values for the severity of competition experienced by the more competitive component were essentially similar ($P > 0.1$), regardless of whether the components shared aerial resources (0.11), soil resources (0.24) or both aerial and soil resources (0.22). However, the mean value of the severity of competition experienced by the less competitive component was greater ($P < 0.001$) when the components shared soil resources (0.85) than when they shared aerial resources (0.46), and was greatest ($P < 0.01$) when components shared both aerial and soil resources (1.19). The severity of competition for soil resources was greater than that for aerial resources in 44 cases, compared with only 6 cases where the reverse occurred (Table 2a). Similarly, in additive experiments where only one component was measured (Table 2b), the mean severity of competition experienced by that component was greater ($P < 0.001$) when the components competed for soil resources (1.15) and for both soil and aerial resources (1.54) than for aerial resources (0.05). Except for the severity of competition for aerial resources, these values are greater than those presented above for the less competitive components. This probably reflects the fact that the various studies of single components were all of young seedlings growing among established plants, whereas in the other studies, components were of the same age.

We have already seen that the severity of competition experienced by a component is affected both by the degree of resource complementarity between components in the mixture, and by the relative competitive abilities of the components. Because components generally competed more intensely for soil resources than for aerial resources, i.e., RYT values were lower (Table 3), and differences between components for root competitive ability were greater than for shoot competitive ability (Table 3), it is not surprising that the severity of inter-component competition for soil resources was usually greater than for aerial resources.

Identifying limiting resources

Separating the effects of shoot and root competition is only the first step towards identifying the limiting resources for which plants compete. Competition between plants for a resource only occurs if (1) that resource is in limiting supply, and (2) the use of that resource by one plant reduces the supply to adjacent plants. Many factors of both the aerial environment and the soil environment affect the performance of plants, but competition does not occur for all these factors.

Above-ground and below-ground factors

Many factors of the aerial environment affect plant performance, e.g., radiation receipt, spectral distribution of radiation, daylength, the temperature and relative humidity of the air, wind speed, CO_2 concentration/and aerial pollutants. Most of these factors cannot be

regarded as resources, since they are not used by plants; for example, plants do not use temperature, relative humidity, wind speed or pollutants, so they cannot compete for these factors. Although CO_2 is used by plants, and often occurs in the air at concentrations that limit plant growth, plants rarely compete for CO_2, because depletion of CO_2 by one plant does not usually reduce the supply to adjacent plants, because of the effects of air turbulence. Many ecologists have referred to competition for aerial space, but there is no evidence that such competition occurs. Plants normally fill less than 10% of the available aerial space, so it is difficult to imagine how competition for space could occur, and the only aerial resource for which plants normally compete is light.

Many factors of the soil environment also affect plant performance, such as the availability of soil water, of macronutrients (e.g. N, P K, Ca, Mg, and S), of micronutrients (e.g., Zn, Cu, Mn, Fe, B, Mo, Cl, Na, and Co), and of soil toxins (e.g., Al, Pb, H, Cd, Cr and Ni), as well as the concentration of O_2 and CO_2 in the soil atmosphere, and soil temperature. Once again, some of these factors (e.g., soil temperature, CO_2, and soil toxins) are not resources, and so are not competed for. Some soil nutrients may be present at deficient concentrations in the soil, but still are not competed for because the use of that nutrient by one plant does not affect the supply to adjacent plants. This is especially true where large reserves of the nutrient are held on exchange sites and where the nutrient is only weakly mobile in the soil solution (Baldwin 1976; Nye & Tinker 1977; Caldwell, 1988). Competition is most likely to occur for nutrients that are required in large quantities, are mainly present in the solution phase, and/or are only slowly released into the soil solution, e.g., N & K. Competition is also likely to occur for soil water, so root competition may be for any one of a number of resources.

Competition for resource

In addition to the experimental separation of shoot and root competition, efforts have been made to identify the limiting resource(s) for which plants compete by inferences based on (1) correlations between plant response and plant attributes, (2) effects of resource supply on competition, (3) effects of competition on resource capture, and (4) effects of competition on plant physiological status.

Correlations between attributes and response

Various attempts have been made to correlate the competitive ability of species or cultivars with particular plant attributes, such as plant height or root size, and so to infer the nature of competition between plants. However, such correlations, like all correlations, should be treated with great caution. Correlations are a useful tool for constructing hypotheses, but the hypotheses must then be experimentally tested.

Manipulation of resource supply

About half the studies comparing shoot and root interactions, which are reviewed here (Table 2), have included variation in the supply of a potentially limiting environmental factor. The most common variables were mineral nutrients (Table 2), especially N, but one study varied soil water content and one varied temperature and daylength. Such studies

can provide evidence on whether the variable (1) is a limiting factor, i.e., whether it affects the yield of the monocultures, (2) affects the relative competitive abilities of the components, i.e., affects C_b values, or (3) affects resource complementarity between components in the mixture, i.e., affects RYT values. The effect of a variable on monoculture yield, whether in an additive or replacement design, provides evidence on whether a factor is limiting, but not whether there is competition for it. The effect of a variable on competitive ability provides no valid evidence on whether the components compete for that variable, even in additive designs (see below). The effect of a variable on resource complementarity can only be interpreted in additive designs, when it provides some evidence of whether there is competition for the variable or not, but the results must be interpreted with care (see below).

There is ample evidence that various environmental factors affect plant growth in monocultures and also affect the relative competitive ability of the components in mixtures, yet are not the object of competition. For example, temperature and daylength (e.g., Eagles 1971; Harris et al. 1981; Christie & Detling 1982), pathogens (e.g., Groves & Williams 1975; Burden et al. 1984; Paul & Ayres 1986), aerial CO_2 concentration (e.g., Patterson et al. 1984; Wray & Strain 1987), and salinity (e.g., Gupta & Ramakrishnan 1977; Barbour 1978; Suehiro & Ogawa 1980) all affect both monoculture yield and relative competitive ability, even though there can be no competition for them. It is therefore clear that no inference can be drawn on whether competition for a given resource occur or not, simply from the fact that the resource or factor affects monoculture yields and/or the competitive ability of components.

The effects of resource supply on resource complementarity provide inadequate evidence for determining if it is the object of competition, even in additive experiments. For example, studies by Donald (1958) and Tofinga (1990) both showed that additional N supplies greatly reduced RYT, i.e., increased competition, when only shoot competition occurred, but had little or no effect when only root competition or both root and shoot competition occurred. The fact that N, a below-ground resource, reduced resource complementarity above-ground, but not below-ground, indicates the difficulty of interpreting such evidence.

Resource capture

Numerous studies have used comparisons of resource capture in mixtures and monocultures to infer competition for a particular resource. For example, light interception by components has often been estimated, by measuring the leaf area of the components and light intensity in the various strata of the canopy (e.g., Schwank et al. 1986); models of competition between components for light have then been constructed (e.g., Trenbath 1986). Similarly, the capture of various mineral nutrients by the components has often been measured, by measuring total biomass and nutrient content. Such measures of resource capture provide no valid evidence of whether or not the components compete for that particular resource. For example, in all the various studies of competition between invading seedlings and established swards (Table 2b), shoot competition greatly reduced light capture by seedlings, but there was little evidence of shoot competition in any of the studies, though there was strong evidence of root competition.

The use of labeled resources, such as ^{32}P and ^{33}P (e.g., Caldwell et al. 1987), provides additional information of competition, but still does not provide unequivocal evidence of competition for that resource. Similarly, the use of ^{15}N, in mixtures of legumes and non-legumes (e.g., Ofori et al. 1987; Tofinga et al. 1993), provides useful evidence of the source of N used by the components, and so may indicate the nature of resource complementarity.

Plant physiological status

Various plant measures provide evidence of the physiological status of the plant, and hence evidence of the factors limiting plant performance. For example, concentration of particular nutrients in plant tissues provide some indication of whether or not the plant is adequately supplied with that nutrient; similarly plant water status indicates whether it is adequately supplied with water. Similarly, the ratio of root weight to shoot weight indicates whether the plant is limited by above-ground or below-ground resources; high root:shoot ratios usually indicate that a soil factor limits plant growth, whereas a low rootshoot ratio indicates that light is the main limiting factor (Wilson 1988b). By comparing plant nutrient concentrations in monocultures and mixtures, inferences have been drawn about the nutrient for which competition has occurred. Similarly, but to a lesser extent, differences in plant water status have been used to infer competition for soil water. Differences in root:shoot ratio have been used only rarely. Such comparisons between mixtures and monocultures should only be made in additive designs, where intra-component and inter-component competition are not confounded, and care should be used in interpreting changes in plant physiological status, because physiological response is complex, and several factors may interact in affecting plant physiological status. Nevertheless, comparison of the plant physiological status of plants in mixtures and monocultures is probably the most useful method of defining the resource(s) for which components compete, though the other methods (i - iii) may help to confirm the definition.

Although partition experiments have provided ample evidence of the importance of root competition, and of its importance in determining resource complementarity, competitive ability and the severity of competition (see above), few if any studies have unequivocally defined the resource for which competition occurred.

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Intercropping in Cropping Systems: Major Issues and Research Needs

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Abstract

This paper tries to put intercropping into perspective with other, sole crop systems. It emphasizes the importance of competition and the sharing of resources between component crops in intercropping. On a crop, or area, basis at least one, and usually each, component will have less total growth, and therefore less root growth and less N-uptake, than a sole crop. However, because competitive abilities of component crops may differ, an individual plant of a given component may have greater or less total growth, root growth, and N-uptake compared with sole cropping. Complementary resource use by the different components may increase their combined total growth, root growth, and N-uptake compared with sole cropping.

Complementarity occurs when components use resources differently. Examples are given of large yield advantages due to greater interception of light over time because of temporal complementarity between component canopies. Comparable effects may be possible below ground if temporal differences in root growth ensure fuller use of water and nitrogen during the season. Similarly, better spatial use of light by "two-tier" canopy systems suggests the possibility of better use of below-ground resources by, say, a combination of shallow and deep rooting components. However, it is stressed that such spatial effects may depend not only on the spatial separation of components but also on those components having other characteristics that make them particularly suited to the specific niches they occupy.

It is stressed that management factors such as population and spacing can influence N-use because of differential effects on competitive ability and growth of individual components. The application of N-fertilizer is obviously a crucial management factor. While there is evidence that dominant components growing much like their sole crops may have similar N-requirements and show similar responses to sole crops, more information is needed on the requirements and responses of components that produce only "partial" crops; there is a similar lack of information on the effect of N-application on the balance of components.

Brief reference is made to the evaluation of intercropping compared with sole cropping. It is proposed that the LER is best regarded as a measure of the basic biological efficiency of a given system. Although the array of other indices may be confusing, evaluations that aim to go beyond

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basic biological efficiency, e.g., for a more applied assessment, cannot avoid supplementing the LER analysis with other indices. Specifically for N-effects, the importance of long-term evaluation over several seasons is emphasized.

Introduction

The aim of this paper is to help put intercropping into context with other cropping systems, which by inference are essentially various sole crop systems. Most of the topics that are considered have already been referred to in the individual papers presented in Session II of this book. In the first section of this paper, some background comments are made on the nature of intercropping in terms of how it differs from sole crop systems, expanding on the theme introduced in the paper by Anders et al. (1996). Ito et al. (1996), in their paper in Session I, quite rightly emphasized the need for more studies on below-ground aspects, and this first section pays special attention to below-ground factors that need to be considered when discussing root systems and nitrogen. This first topic leads directly to the second, that of complementarity, which is a fundamental feature of intercropping and which was a subject of some concern in several sessions of the ICRISAT Workshop; again, special attention is given to below-ground aspects. Third, comments are made on the importance of crop management practices, aspects of which were presented in the papers by Potdar et al. (1996) and Ali (1996). General implications concerning management regimes in intercropping research are also highlighted. Finally, consideration is given to the evaluation of intercropping and the kind of comparisons that need to be made with sole crops to determine the relative merits of these systems.

In this overview paper, no attempt is made to provide a critique of the individual papers presented in Session I. These are simply used as a basis from which particular themes or principles can be drawn and from which further comment can be developed. Where relevant material discussed in other Sessions has also been drawn on.

Two cautionary comments must be made at this point. The first is that there is a need to be cautious when trying to extrapolate the results of specific intercropping studies. Intercropping embraces an almost infinite range of different situations made up of different crop combinations, environments, and management practices. Researchers have to be particularly wary of generalizations of the kind that imply, for example, that particular benefits or processes hold true across intercropping as a whole. The consequence of this for research objectives is that there is a need not only to elucidate those basic principles that can be broadly applied, there is also a need to determine how factors of crop, environment, and management will modify the application of those principles in practice.

The second note of caution is that when considering the importance of only one specific aspect, in this case nitrogen (N), intercropping should not be judged by that factor alone; whether a given intercropping situation is worth growing or not will be determined by several factors. For example, the existence of N-transfer in a given cereal/legume intercrop may not make that situation worthwhile if there is some overriding disease problem. Conversely, in the absence of a N benefit there may still be other factors that ensure an overall net benefit. This does not in any way minimize the importance of the N

factor but it is a reminder that N research is essentially helping to build a broader intercropping picture rather than determine whether given intercropping situations are or are not worth growing.

The nature of intercropping

Intercropping is distinguished from sole crop systems in that there are two or more crops growing on the same piece of land at the same time with the result that there are interactions between them. From the viewpoint of root growth and N, the key interaction that occurs between the crops is competition. Donald (1963) described competition between different plants of the same species as the situation when the availability of a resource falls below the combined demands of the individual. This definition highlights two fundamental principles of competition that can be extended to intercropping.

1. *On a crop, or area, basis at least one* (*and usually each*) *component obtains less resources than it would as a sole crop and it therefore produces less yield than a sole crop,* (In practice, this reduction in yield due to competition is commonly accentuated by the plant population of a component being less in intercropping than in sole cropping.)
2. *On an individual plant basis, because of differences in the competitive ability of the components, a given component may experience less or more competition than in a sole crop and, respectively, obtain more or less resources and achieve greater or smaller yield per plant,* (In fact, the yield per plant can increase only if a component has a lower population than in sole cropping, which is not always the case. If a component has the same population as in sole cropping the presence of another component can only increase the competition and therefore decrease the yield of the individual plant.)

However, these two principles only indicate how resources must be shared between components, as they might be between different plants of the same species. A crucial principle that applies to competition between different species is:

3. because of complementary effects in the way resources are used by different components, overall resource use may be enhanced compared with sole cropping and the combined yield of all components may be greater than from sole crops. Relating these three basic principles specifically to root growth (and with the same provisos with regard to plant population):

* *the total root growth of a given component crop will usually be less than its sole crop;*
* *the root growth of individual plants of a given component may be greater or less than in sole cropping; and*
* *the combined root groxvth of all components may be greater than sole crops.*

These are very simple principles but they have crucial implications for N-use. The concept of components having to share resources and a given component having less root growth and less total yield than in sole cropping implies less soil-N uptake by that component. This is important to remember when evaluating component performance in terms of uptake because clearly a component producing only a "partial" crop can not be expected to take up as much N as a sole crop. By the same argument, a legume component that is only a partial crop can not be expected to fix as much N as a sole crop. The concept

of different competitive abilities resulting in greater or less root growth of the individual plant means that individual plants may have better or poorer access to soil-N, and this has implications for the N-status of the individual plants. This is the basis of the "sparing" effect that can occur in cereal/legume systems that replace some of the cereal with a legume and therefore allow individual cereal plants greater access to soil-N. And of particular importance, the concept of complementarity allowing greater combined root growth and yield implies greater combined nitrogen uptake than sole crops.

Complementarity in intercropping

The principle of complementarity is that when there are differences in the way components use resources these differences may complement each other and achieve better combined resource use than can be achieved by sole crops. It is worth emphasizing that complementarity can be, and probably most often is, a purely passive mechanism in that it does not require one component to directly effect another; it simply requires components to behave *differently.* For example, complementarity between root systems does not require the roots of one component to exert, say, a chemical influence on the roots of another component.

Most evidence for complementarity has come from canopy studies, and a useful approach is therefore to consider what findings from these might be extrapolated to root systems. However, complementarity is probably best considered as occurring between *plants as a whole,* not *either* canopies *or* root systems. In particular, there may be little value in trying to ascribe intercropping advantages exclusively to either above- or below-ground complementary effects since almost certainly there has to be interdependence between these. For instance, a higher yield from intercropping means that there has to be greater growth both above- and below-ground than can be achieved by sole cropping; presumably, therefore, there has to be some kind of complementary effect both above- and below-ground for the greater above- and below-ground growth to occur.

Temporal complementarity is the best documented mechanism for bringing about higher yields in intercropping. This is where the growth cycles, and therefore the major resource demands, of components differ in time, as for example in the sorghum/pigeonpea system where maturity periods of the two components are typically 100 and 180-200 days, respectively. The main effect of this complementarity is usually that intercropping makes fuller use of resources over time than can be achieved by sole crops. Light, which has to be instantaneously intercepted if it is to be utilized at all, is the obvious resource that would be expected to be utilized more fully due to temporal complementarity, and indeed appreciably greater capture of light has been shown in temporal systems such as the sorghum/pigeonpea (Natarajan and Willey 1980b). The relevance of temporal complementarity is less obvious for below-ground resources that constitute more of a finite pool that crops can draw on as needed. But it can still be beneficial when there is some temporal element in the availability of below-ground resources. For example, temporal complementarity might ensure fuller use of rainfall over the season, and in drier areas where access to N is limited by water availability this same complementarity might ensure

better use of N. There could also be better use of any N that becomes progressively available from mineralization. Note that temporal complementarity may not have to be so dramatic as that in the sorghum/pigeonpea for it to be beneficial It may well be that a relatively small difference between components in their timings of peak resource use is sufficient to spread demand to beneficial effect.

Possible causes of spatial complementarity can be more difficult to visualize; not surprisingly therefore, spatial complementarity is less well understood. There are however some good examples of canopy effects. Reddy and Willey (1981) showed that a pearl millet/groundnut canopy, in which the millet was typically 150cm and the groundnut about 30-40cm, could improve the efficiency of conversion of light energy by more than 20%, and this was associated with an increased yield from intercropping of the same order. A similar "two-tier" effect is often visualized for intercropping root systems when a shallow-rooting and a deep-rooting component are combined. It is reasoned that intercropping then provides a fuller exploration of the whole profile than can be achieved by separate sole crops. This would seem an acceptable mechanism that might achieve greater use of below-ground resources in many intercropping combinations. However, the inherent assumption in this particular complementary effect is that a given sole crop can fully explore either the upper profile or the lower profile but not both. This assumes, therefore, that the deeper rooting component does not also provide full exploration of the upper profile, which may not always be the case.

When considering this "two-tier" mechanism in relation to N-use it may be worth re-emphasizing the link with water. In rainfed situations, the available water may be at different depths in the profile at different times, depending on the particular wetting and drying cycles. Given that these cycles are unpredictable, it might be particularly beneficial for both water and N-access to have a fuller distribution of roots throughout the whole profile, as is being visualized here for intercropping systems.

However, this comparison with the canopy situation needs closer scrutiny. In reality, the canopy effect quoted above is probably attributable to a combination of differences between the two components. The height difference is the obvious one, which provides the "two-tier" spatial distribution, and this in itself might well contribute to greater efficiency of light use by ensuring greater penetration of light into the canopy and therefore better dispersion over more leaves. But historic evidence from research on sole crop canopies suggests that the effects of canopy dispersion per se are limited. Almost certainly, therefore, the very large increase in efficiency in the millet/groundnut system is due to the combined effect of the different distribution of the canopies and the different characteristics that make each component particularly suited to its own height niche. Thus the tall, erect-leaved, C_4 millet is particularly suited to the high light environment at the top of the canopy whereas the low, compact, C_3 groundnut is more suited to the low light environment at the bottom of the canopy (Reddy and Willey 1981). If this reasoning has any parallel below ground it means that the possible benefits visualized above because of differences in the distribution of component root systems might be enhanced by interaction with other differences between components that make them particularly suited to different soil niches.

A further aspect of this complementarity due to different rooting depths has been postulated (Whittington and O'Brien 1968; Fisher 1977), which is the possibility that a

deeper rooting component might be forced even deeper because of competition from the shallower rooting component. This would obviously enable the intercropping system to gain access to additional resources that were not available to the sole crops. The effect would seem to be more likely when the deeper rooting component is slower growing and is still producing its root system after the earlier, shallower-rooting component has depleted the upper soil layers of nutrients and water. Natarajan and Willey (1980a) could not detect this effect in sorghum/pigeonpea, a combination that would appear to have all the right characteristics. The recent detailed root studies reported at this Workshop have similarly failed to show any real evidence of the effect in this same sorghum/pigeonpea combination (Katayama et al. 1996).

Despite the importance always attributed to differences in root distribution, there seems little reason why this should be the only basis for complementarity between root systems. It was stressed earlier that complementarity depends on *differences between* components and during the Workshop many researchers emphasized the complexity of root systems and the many characteristics that may differ between species, e.g., rates of activity and response, competitive ability for N, abilities to utilize nitrate or ammonium nitrogen. Far from being dependent on distributional differences in root systems, some of these characteristics could well require a close intermingling of root systems to allow complementarity to enhance resource use. This suggestion is obviously rather speculative, but note that one of the most clearly established phenomena of intercropping root systems is that root densities can be considerably higher than in sole crops (Natarajan and Willey 1980a; Gregory and Reddy 1982; Katayama et al. 1996). Therefore, there is clearly some mechanism that allows a given volume of soil to support a greater mass of roots when those roots are a mix of different species than when they are from a single species. The possible occurrence of this kind of complementarity is surely worthy of greater research attention.

A very specific form of complementarity of N-use is of course that which can occur in legume/non-legume systems. These systems are considered in detail elsewhere in the Workshop so they are used here only as an example. The basic mechanism of complementarity is in fact particularly well illustrated by the "sparing" effect, i.e., when the legume satisfies some of its N-requirement by fixation and allows the non-legume to use more soil-N. These very marked differences in N-use provide a very obvious source of complementarity that can result in greater combined use of N; and this basic mechanism of complementarity is not of course dependent on any of the fixed-N being transferred to the non-legume.

Crop management factors

Attention to crop management is just as critical in intercropping systems as it is in sole crop systems. There can be additional complexities of course because optimal production from the system as a whole can only be achieved by establishing an appropriate balance between the requirements and responses of the different components. Many management factors are likely to interact with aspects of N-use. This can be particularly true for plant population

and spacing; this factor has enormous influence on the competitive ability and growth of the different components, which in turn can determine the extent to which complementarity can be expressed and increased yields can be achieved. For example, the paper by Potdar et al. (1996) in this Workshop illustrated how changing the proportional population of components could effect the performance of a pigeonpea/cotton system.

But the most critical management factor when considering N-economy is the use of N-fertilizer; the requirement for this in intercropping systems is still poorly understood. Several researchers have shown that N-requirements of intercrop components can be very similar to their sole crop requirements (Rao and Morgado 1984; Rao et al. 1987). But this has been when the components are the dominant ones with the same plant populations in intercropping as in sole cropping, and thus the components would normally be expected to yield as well as sole crops. In such instances these components are virtually growing as sole crops and, predictably, are responding to management factors in a similar manner. What is much less predictable however, is the way in which N-requirements are modified for components that are grown only as partial crops, especially if they are then dominated. This is where there is a need to elucidate how N-requirements are modified in relation to particular characteristics of intercropping systems.

A similar situation exists in non-legume/legume systems, where the general effects of applying N are well known but there is a need to clarify relationships that determine actual N-requirements in particular circumstances. The most common effect is that application of nitrogen increases the growth of the non-legume but this in turn, because of increased competition, decreases the growth of the legume (Rao and Morgado 1984; Rao et al. 1987). A basic objective should be to try to maintain a desirable balance between the components to preserve the complementarity referred to in the previous section. More could be done to adjust spatial distribution of the components to enable N to be targeted more specifically at the component that needs it. For example in the 2:1 row arrangement commonly used in sorghum/pigeonpea combinations, N can be conveniently applied between the two sorghum rows to make it readily available to this crop but to keep it away from the pigeonpea. This type of approach needs to be combined with studies on optimum rates of N, especially, as emphasized above, when reduced populations are used for the non-legume components and their N-requirements are therefore not easily predicted from sole crop situations.

These comments suggest a need for further work to clarify the ways in which different aspects of N-use are modified by management factors. This area of research might well have a wider benefit in helping to bring together two rather extreme approaches that seem to be prevalent in intercropping research at the present time. One is the applied approach that typically compares a large number of management options. The other is the very detailed approach that tries to elucidate, or model, fundamental relationships but is able to relate these only to particular management situations.

The occurrence of interactions between N and management practices also has some general implications for N studies, especially the more detailed studies that can cover only a limited range of management situations. First, as emphasized in the Introduction, caution must be exercised when trying to extrapolate findings to wider circumstances than the particular ones under study. Second, care needs to be taken when deciding "background"

management regimes for N studies. And third, published results should indicate very specifically which management regimes have been used.

Comparing intercropping with sole cropping

As stressed at the outset of this paper, intercropping represents an alternative to sole crop systems. Therefore comparisons between intercropping and sole cropping are fundamental to intercropping research. At several points in the Workshop there were questions raised on what kind of comparisons should be made; therefore, I make some general comments here.

The basic requirement is usually to compare the overall performance of intercropping (i.e., the combined yield of all components) with the yield obtained by growing the component crops in sole cropping. For any given season the standard method of making this comparison, as indicated in the paper by Anders et al. (1996), is to calculate the Land Equivalent Ratio (LER). Use of LER is often questioned, as indeed it was at the Workshop, but these questions commonly arise because of doubts about what LER is intended to measure. The LER in fact assesses what can be regarded as the basic biological efficiency of intercropping compared with growing the components as separate sole crops. An LER greater than 1 for a given situation indicates that in that particular set of circumstances intercropping gives more yield than can be achieved by growing the components separately. In essence, therefore, an LER greater than 1 means that there has been some beneficial complementarity of the kind discussed earlier, and that this complementarity has resulted in the higher yield. In almost any intercropping study this basic check for complementarity and yield advantage would seem to be worthwhile. The importance of this is perhaps most readily appreciated by remembering that the rapid identification of those intercropping situations that do not give an LER greater than 1, and which do not therefore do anything that cannot equally be achieved by separate sole crops, could prevent researchers from wasting time chasing spurious intercropping benefits.

There were also a number of references during the Workshop to other measures of intercropping performance. Anders et al. (1996) quite rightly pointed out that measures other than the LER have been little used, despite the large volume of literature that has been devoted to them. One reason may be that the increasing number of alternative measures has tended to confuse rather than clarify. The fact remains however that if a particular research study needs to go beyond a measure of the basic biological efficiency of intercropping it is necessary to do *something* more than calculate the LER. This is commonly the case for practical evaluations of intercropping when there is a need to take into account such factors as economics, nutritional values, or constraints on the proportions of component crops that are acceptable to farmers. For more detail on these analyses readers are referred elsewhere (Willey 1985). For present purposes, suffice it to say that these more practical measures should seldom replace the LER, they should *supplement* it.

However, when soil factors such as N are being considered, comparisons between intercropping and sole cropping systems cannot be confined to effects within a given season - they must include residual effects across different seasons. For example, it is well

recognized that in many intercropping systems that include a legume component the fixed-N is more likely to benefit subsequent crops than the component growing with the legume. Evaluation of such systems clearly must include the period over which residual effects might occur. This particular example also illustrates how this longer term evaluation must still be based on a comparison with sole crop performance. This is because the transfer of fixed-N per se, whether to crops growing in association or to subsequent ones, does not necessarily mean that intercropping is providing a N-benefit compared with sole cropping. Strictly speaking, such a benefit can be said to occur only if this transfer is greater than can be achieved from a sole crop rotation of legumes and non-legumes, a system in which fixation and subsequently released N might well be greater because the legume is freed from the competition of another crop. This was the kind of long-term comparison made in the paper presented by Potdar et al. (1996), and which enabled them to show that a rotation of sole crops of cotton and pigeonpea were better than various "strip-crop" intercropping systems of the two crops.

The uptake of soil-N and the long term effect of intercropping on soil-N status is another area requiring evaluation over more than one season. Intercropping systems that produce higher yields than sole cropping, as a result of the kinds of complementary effects discussed earlier, inevitably take up more N. And there is a crucial, unanswered question as to the long-term effect these systems have on soil-N. It is possible that some of the additional N taken up by intercropping would normally be "wasted" by sole crops. For example, a more "efficient" root system in intercropping (e.g., because of the greater root densities referred to earlier) could result in less loss of N by leaching, or some N might be taken from greater profile depths (if intercropping forced root systems deeper than sole crops, as was discussed earlier). On the other hand, some of the additional N taken up could obviously be the result of a greater demand on the normally available N, which would in effect be a " mining" of soil-N and thus produce a decline in N-status. These effects can only be fully elucidated by long-term studies comparing intercropping with sole crops. Such studies can require a major investment in land and labor resources but they are urgently needed. The long-term ICRISAT experiment reported by Rego and Seeling (1996) at this Workshop has shown that dramatic long-term changes in soil nitrogen status can take place under cropping systems involving different proportions of legumes. This experiment was not set up to make the specific intercropping and sole cropping comparisons referred to above but it illustrates the general approach needed in long-term systems experiments; it also illustrates the very valuable information that such long-term experiments can provide.

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Root Dynamics in Natural and Agricultural Plants, and the Making of Domestication

F. Zucconi[1]

Abstract

The raising of monophytic crops in agriculture has deprived plants of the advantage of a diversified biomic[2] stands, thus requiring an adaptation to the new ecosystem. In particular, it demands an adjustment tozvards a root residentiality*, and a decreasing interactiveness with other organisms. The result is a selective pressure opposite to that existing for natural plants in cenoses*, where interactiveness and root dynamics are maximized. However this adaptation favors the formation of a small residential root system (Root) that is less demanding in energy and leads to the establishing of an efficient agriculture phytotype*. In this report, the inevitability of the process is analyzed by describing (a) the dynamics of root development and (b) its equilibrium with soil constraints, (c) the mechanism of soil sharing between roots and (d) its role in the formation of cenoses, and (e) the implications of missing such interaction in agriculture.*

Consequences on the environment will also be analyzed, as vegetation changes brought by agriculture produce feed-back effects that lead to a reduction in saprophytes and lower the humification process. Such changes work against the plant command of its own trophism. They also cause a compensatory expansion of pathogens and parasites, a great arrassment to agricultural production today. It follows that the selection towards an agricultural phytoptype has possibly been stretched to its utmost adaptability to the ecosystem changes brought by cultivation practices, and any further pressure might easily lead to a rapid loss in efficiency. Consistently, the exiting insistence on fewer extensive crops and the increasing genetic standardization are possibly putting the agricultural process beyond any acceptable minimum equilibrium, thus bringing the sustainability of the cultivative model at risk.*

Premise

Agricultural plants make up a distinctive group, differing from natural species in their selective adaptation to the environmental conditions set by cultivation practices. In particular, the raising of crops in cleared up soils simplifies the formation of the root system

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(Root) and eliminates competition with a standing vegetation. However, it deprives plants of (a) the reciprocal supportive role existing in cenoses, with their asset of a rich saprophytic-symbiotic life, and (b) the control of humification and of natural suppressiveness of pest agents. Cultivation practices imperfectly redress such a deficiency, requiring compensative changes in the Root and in turn in the crown (hereafter, simply called Shoot) and in the reproductive cycle. The steps of such changes, comprehensively called *domestication*,* are most evident in trees which have distinct life stages and great territorial spread, thus also offering a valuable model in this analysis. On the other hand, natural annual species share a number of common characteristics with cultivated plants: this suggests the existence of some parallel evolutionary trends, and justifies the role of such plants at the onset of agriculture (Section 6.1).

The physiological and ecosystemic roles of the Root in the colonization of the land are indeed relevant, along this evolution, being responsible for (a) adapting plants to soil variability, (b) determining most of their interactions in cenoses, and (c) compensating for the loss of such interactions in agriculture. To pursue this line, then, it.is necessary to grasp events belonging to plant physiology, root trophism, and phytocenotic aggregation. Mostly, it requires grappling with the interactions of such events, and with the multiple alternative scenarios that can be generated. Consistently, this paper describes the dynamics of root through: (a) the balance between the plant's striving for growth and soil constraints; (b) the mechanism of soil sharing between plants, and (c) its role in the formation of cenoses; and (d) the formation of a new agricultural phytotype with (e) its assets and liabilities. Above all, the discussion runs at a *systemic** level, aiming to define (a) principles of plant behavior, (b) *homeostases** that regulate such behavior, (c) *homeorheses** that evolve between homeostases, and (d) conditions that affect such evolution.

Root size and root activity

Root-Shoot homeostasis

The attempt to estimate or predict the size of a Root requires an understanding of how the plant itself may control it, and which factors enter into the decision. Indeed, Roots vary greatly in their mass, shape and distribution, reflecting environmental conditions, Shoot size, and plant age. An analogous conclusion, in reverse, holds for Shoot size. Complying with such variables, the plant regulates Root and Shoot growth by the integrative role of internal correlations and, in particular, by two mutually limiting conditions: (a) the plastic request in both Root and Shoot for their combined product (i.e., *edaphic correlation*),* and (b) the possibility for each organ to control only its own product formation (Zucconi 1994a). The result is the onset of a bipolar (contrastive) regulation in which each organ conditions the growth and activity of its partner, by its own product, and is in turn influenced (feedback) by the activity of the partner itself.

2 This paper proposes a new approach to the study of the root, requiring the redefinition of some scientific terms and the making of new ones; both are marked by an asterisk (*) at their first appearance, and one listed in a glossary at the end of this chapter.

Consistently, there will exist a product exclusively or preferentially (more efficiently) yielded by the Root, that will exert a limiting role on the development of the Shoot. Considering its complexity and variability (through environments, seasons and age), such a product will be comprehensively termed the below-ground factor, or *ipogean factor**,* or I-factor (Zucconi 1992b, 1994a, b). In parallel, there will exist a complex and variable above-ground product of the Shoot, or *epigean factor** (E-factor), that plays a limiting role on Root development. The contrastive role of I and E factors generates a circular action-feedback relationship, setting up a remarkably simple homeostasis (Fig. 1) that governs the whole plant as a system and commits its organs to a complemental growth. The result is also a plastic equilibrium that allows the plant to adapt to variable conditions. An example is the response to grafting on a dwarfing rootstock. Shoot and Root size in the resulting chimera are mutually influenced by the two grafted organs (Fig. 2), while differing from both parent plants.

Limits of modeling by the root/shoot ratio

Root and Shoot grow coevally during a plant's life, although according to different rates, as the plant develops a relatively large Root in its young or juvenile stage and a large Shoot at reproductive maturity (Fig. 3, above). The result is a gradual decrease in Root/Shoot (R/S) ratio that reveals a greater supportive role of Root activity in young rather than in mature plants. Most importantly, the onset of maturity occurs independently of any absolute mass of the plant, being related to the R/S ratio and, precisely, to its decrease below a minimum critical level or critical mass* (Zucconi 1994a). Indeed, the critical mass acts as a limit above which the plant persists in its vegetative stand, and below which turns to a stable reproduction (Fig. 3, below). This mechanism, then, supplies an important key for

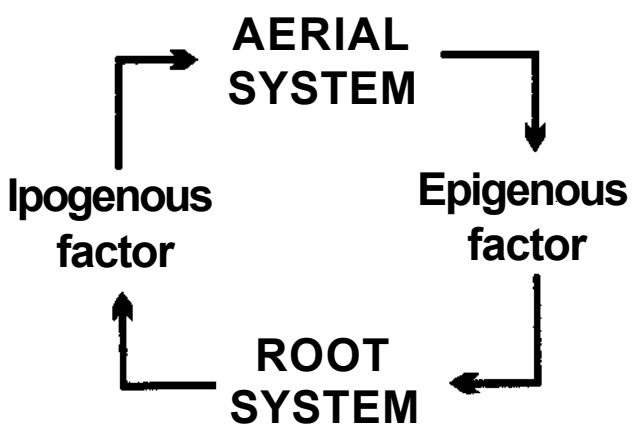


Fig. 1. Homeostatic balance of Root and Shoot development through the limiting role of their products (epigean (E) and ipogean (I) factors, respectively).

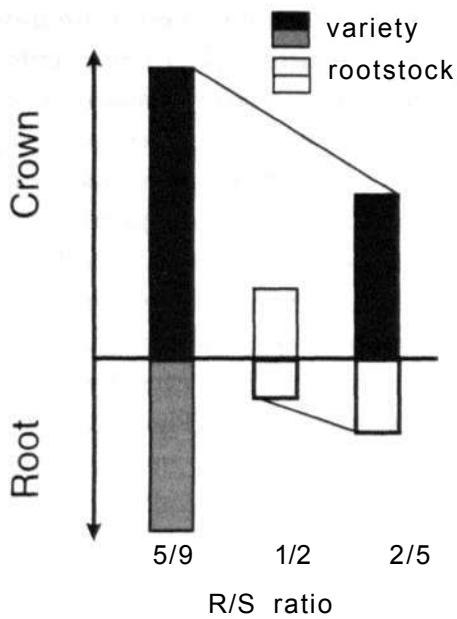


Fig. 2. Grafting on a dwarfing rootstock imposes adaptive changes, with the crown growing smaller than on its own roots, and the Root growing larger than under its own crown. (Adapted from Zucconi 1992a).

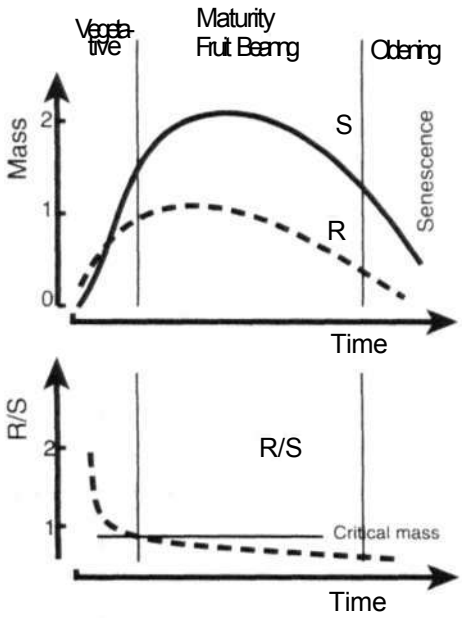


Fig. 3. Above; Time course of root and shoot size during a plant life-cycle. Below: The R/S ratio decreases steadily, causing a shift to a reproductive maturity when a critical mass level is reached. (Adapted from Zucconi 1992a).

physiological understanding, as well as a basic tool for an *external* control of the plant.

A flexible onset of maturity allows the plant to adapt to environmental resources or constraints (e.g., soil volume: Fig. 4), or yield to other conditions (Fig. 2). The strength of this adaptability is proven by observing how artificial changes that set the R/S ratio above

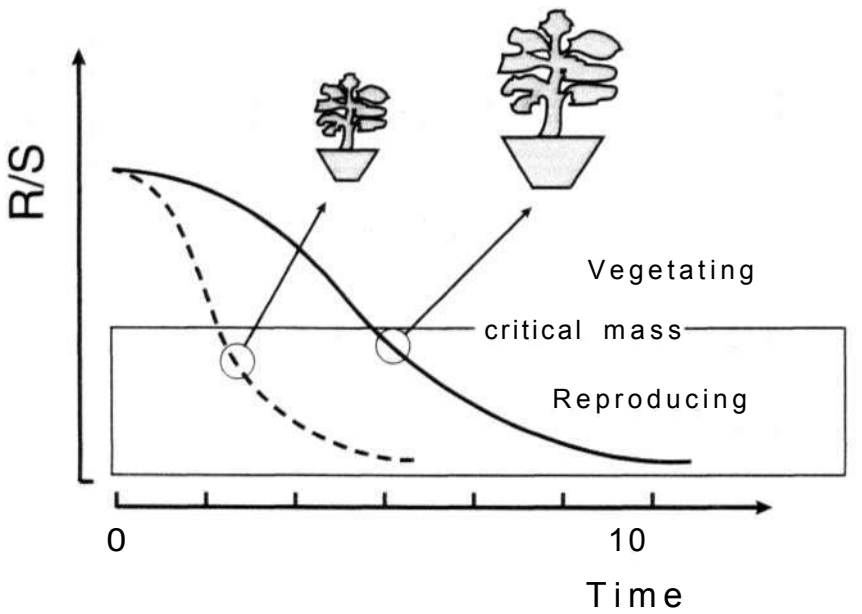


Fig. 4. The critical mass for reproduction may be achieved at an earlier or latter time according to Root expansion (pot volume), bringing about changes in plant size.

or below the critical mass also induce responses which in fact are predicted by the model itself. Thus, increasing the R/S ratio by extensive Shoot pruning (from {R/S} to {R/s})[3] restores the vegetative strive in a mature plant, and denies reproduction. This condition lasts till the plant recovers its critical mass ((R/S)). The opposite occurs with a Root containment in a pot that hasten the critical mass. This mass then is achieved with a smaller plant, inducing dwarfing.

From a *cybernetic** view point, the representation of the plant through the dynamics of its R/S ratio provides an evocative but approximate approach to the understanding of regulative events. This because Root and Shoot masses remain highly variable under the influence of environmental conditions and age (i.e., differential accumulation of dead wood). Consistency with the homeostasis of Figure 1 commands more attention to the relative activity of such organs, as their products', rather their mass, enter the correlative control. Indeed, it is the products' exchange that induces compensatory changes in the mass of the organs, to maintain a constant activity vis-a-vis variable external conditions. Thus the plant, aiming at a given Root activity, will compensate for the existence of favorable or unfavorable soil conditions by setting, respectively, smaller or larger Roots, while keeping a constant Shoot. The evolution of physiological age, too, remains independent from the R/S ratio, rather determined by the ipogean/epigean factor (I/E) ratio. In conclusion, Root and Shoot masses (M) maintain a role which, however, they exert along with that of their activity (A), and with transport (T) to and from each organ. The level of this I/E ratio in a given organ may then be expressed as:

3 In this analysis, curly brackets refer to physical quantities, and capital or small letters express relatively large or small values (Zucconi 1992b), The R/S ratio expression will still be used in its abstract value.

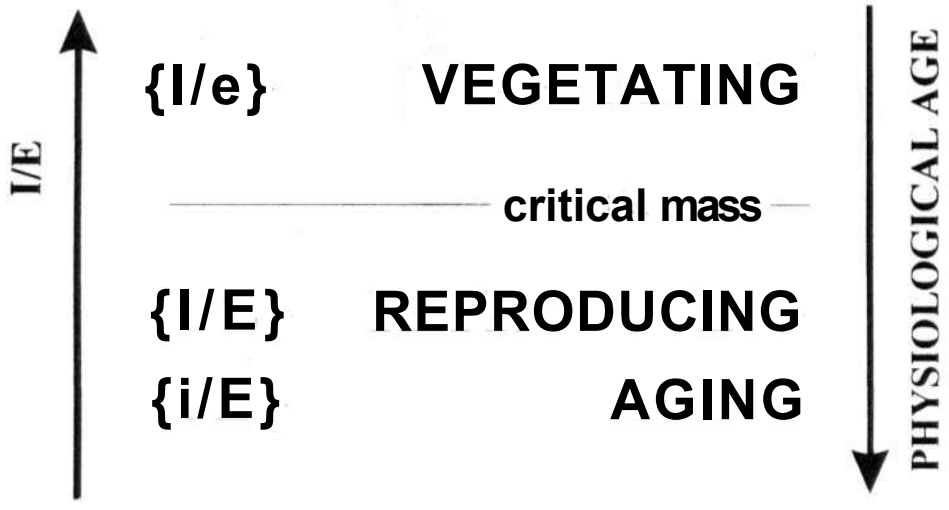


Fig. 5. I/E ratio in Shoot. The reproductive stage may be achieved independently of the mass of Root and Shoot when their product (I/E) ratio falls below a critical mass.

$$I/E = f\ (M, A, T) \qquad (1)$$

The I/E model simplifies the analysis of the R-S communication (Zucconi 1994a), and relates the shift to maturity to the encounter between a decreasing I/E ratio and a specific minimum level, still figuratively termed the "critical mass" (Fig. 5). All this relegates the use of the R-S model to specific comparable conditions, bearing a lower cybernetic applicability than the I-E model. The R-S model should not be abandoned, however, as it is still important in accounting for a number of technical conditions, as in the manipulations of the masses of plant organs by grafting, pruning, etc., that hold the required comparability.

The size of the Root

Both the R-S and I-E models explain the responsiveness of the plant to environmental conditions, as reflected in the plant's strive for achieving maturity independently of its own size, whenever it achieves the critical mass. The impact of the pot volume in limiting the mass of a plant illustrates well this epigenetic* freedom, in which the shift to reproduction is retarded in proportion to the substrate volume (Fig. 4). The same holds with soil fertility (Fig. 6): different Shoot sizes may be obtained, in comparable pot volumes or Root sizes, by varying the nutrient availability. Van der Werf's (1996) inverse relation between soil nitrogen availability and Root carbon requirements is consistent with the requisite for a smaller Root shown in this model.

The size reduction of the plant in response to a decreasing pot volume also accounts for an analogous behavior in the field, where neighboring plants set allelopathic* barriers to the transmigration of roots that act as pot walls. The result is the formation of a virtual

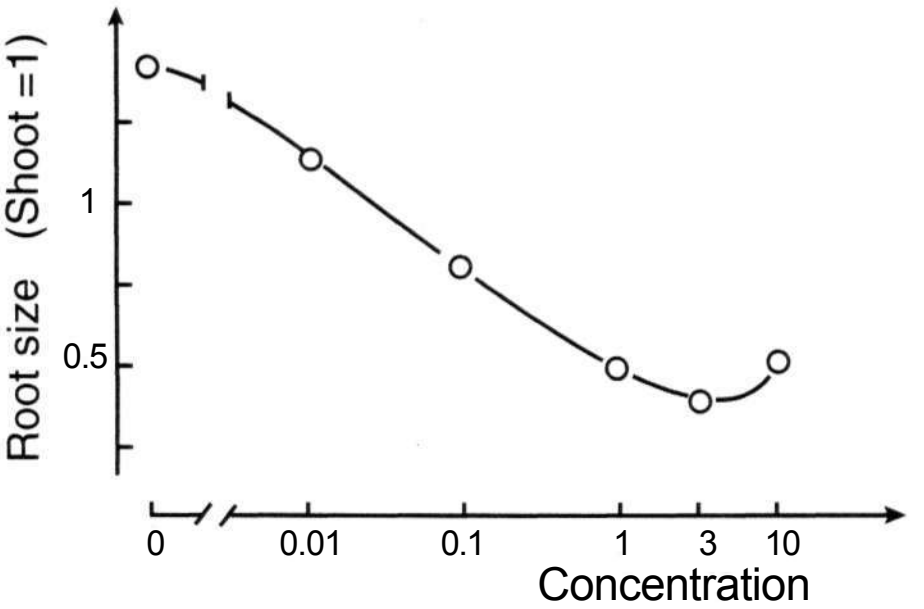


Fig. 6. Root/Shoot ratio in 22-day-old bean plants in contact with various concentrations of nutrient solution (standard concentration = 1). (Adapted from Zucconi 1988)

container, the *allelopathic pot** (Zucconi 1988), responsible for a high plant sensitivity to planting density, as well as to fertilization and irrigation practices. This shows that the total Root size (R) is a direct function of available territory (V) and of Shoot size (S), and is an inverse function of soil fertility (F). Also, R size it is affected by physiological age (Fig. 3), i.e., increasing in a young plant (Ay) and decreasing during the reproductive stage (Ar). These relationships are expressed as:

$$R = f\left(\frac{V, S, Ay}{F, Ar}\right) \qquad (2)$$

Expression 2 is also consistent with the I-E model analysis, in that V and F affect I factor production, S affects E factor production and I factor consumption, and age influences transport (fast in young plants, and sluggish in senescing ones; Zucconi 1994a). The physiological implications of a variable Root size will help in assessing the impact of the cultivative environment in the making of agricultural phytotypes (Section 6.1).

Root growth dynamics and its effectors*

Root absorption constraints

Root development is characterized by an overall dynamism that exceeds that of the shoot, and reflects the peculiarity of its own function and environment. Indeed, while light and

carbon dioxide reach the shoot and allow it to operate in a stable stand, nutrients and water are depleted by the absorbing rootlets at a rate that exceeds that of solubilization and diffusion. Rootlets then need a continuous substrate renovation, a process implying migration and shedding of obsolete absorbing nets. Such a dynamism reflects intrinsic properties of the Root that need a more in-depth analysis.

Root dynamism bears advantages for the plant that include (a) an increased competitiveness for the substrate and (b) the interaction with other species in cenosis. It has its cost, however, as root renovation represents an energy-consuming process. Also, it oldens the soil environment, laden with residues, hampering trophism and adding to the root quest for territorial renovation (Zucconi and Monaco 1987; Zucconi 1992b, 1993). The nature of nutrient depletion and of soil *oldening** needs to be clarified because they affect, in turn, the behavior of roots and the sharing of soil between plants. Soil quality and availability, in particular, impose different root developmental patterns and change Root distribution. The following analysis of root migratory behavior will help revealing these patterns and changes.

Root micromigration*

Root centrifugity*

The dynamics of Root growth is intimately connected with the depletion of soil nutrients. Consequently, a pervasive soil exploration, or micromigration (or simply *migration*),* compensates for the slow solubilization and diffusion of nutrients, causing a progressive root expansion beyond the exploited territory. Through this metastasis, a sizable amount of obsolete degradable residues (soft tissues, mucilages, and exudates) is released in the "old" soil, where it becomes the substrate for a rich saprophytic life. Although conspicuous, the amount of root renovation is hard to assess (35%, 75% of plant energies) due to its variability between soils and the fast degradability of residues. Renovation is reduced in the presence of a high nutrient endowment. This accounts for the smaller Root (Fig. 6) and the reduced micromigratory urge existing in nutrient-rich soils, and more so in humic soils. At the same time, fertilization practices increase absorption, although only amounting to a partial substitute for soil fertility. Also, intercropping with leguminous plants reduces to some extent the root renovation quest (Katayama et al.1996) through the same mechanism. Finally, the migratory urge increases in arid soils, where water scarcity imposes a greater substrate exploration. It also increases in soils with a variable water table, which require a continuous shift in absorbing roots between layers.

The nutrient-seeking urge of the root, although fundamental, does not represent the only effector of Root's expansion. The reason is that, in spite of the tendency of the used soil to soon recover its nutrients' equilibrium, roots do not tend to regress to their former territories. Contrary to this, they persist in a centrifugal stride that lasts up until the Root maintains a high regenerative power. This behavior is explained by the existence of an allelopathic (i.e., *dyspathic*, autophobic**) root repulsion for its territory, when laden with residues, and by the urge for feeding in new territories (Zucconi 1992b, 1993).

Dispathy is tied to the microbial decomposition of root residues, with the release of

metabolites that induce root *dystrophy** and die-back (Zucconi and de Bertoldi 1987). Such allelochemicals are termed *secondary allelopathk factors** (SAFs, Zucconi 1993), and differ from *primary allelopathk factors** (Section 2.3) in their nature and origin. Root sensitivity to SAFs is circumscribed to the species that generated the residues (autophobia), and does not necessarily involve other species, some of which may be compatible *(xenophily*)* with the abandoned territory. Therefore the existence of a specific sensitivity explains the root quest for new soil, and its high turnover when confined to an unrenovated substrates. Crop stunting by soil sickness is also tied to the dyspathic effect of own residues at recropping. On the other hand, the residues from a given species may be accepted by other species, thus accounting for the success of some crop rotation programs.

Evidence against a simple nutritional causation of root expansion comes from observing the plant intolerance for unrenovated hydroponic solutions. Indeed, a plant may spend its entire life cycle in a soil, no matter if poor or unbalanced, and yet it may not stand for more than a few days in an apparently perfect hydroponic solution. The latter requires frequent solution changes to avoid root stultification by the allelochemicals' diffusion in the water; and such changes may not be substituted by any nutrient restitution, pH change, or other correction. In conclusion, trophism requires a control of factors beyond the presence of nutrients, because the existence of SAFs imposes its own limitations on the substrate availability and use.

Consequences of centrifugity

In solid substrates, autophobia and centrifugal stride lead to the "emptying" of the core of the Root space (Fig. 7), which then becomes bare of absorbing roots. This event, defined as *cavitation** of the root system (Zucconi 1988), confines absorbing roots to an expanding periphery which, in an unrestricted territory, appears enclosed in a toric curve (Fig. 8). The

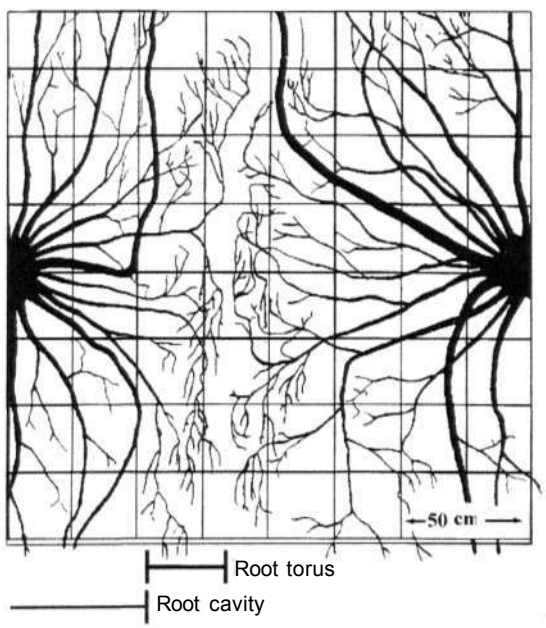


Fig. 7. Authopathic forces compel the root system to expand centrifugally to absorb in ever new territories, leaving a central core void of absorbing roots. (Adapted from Baldini 1976).

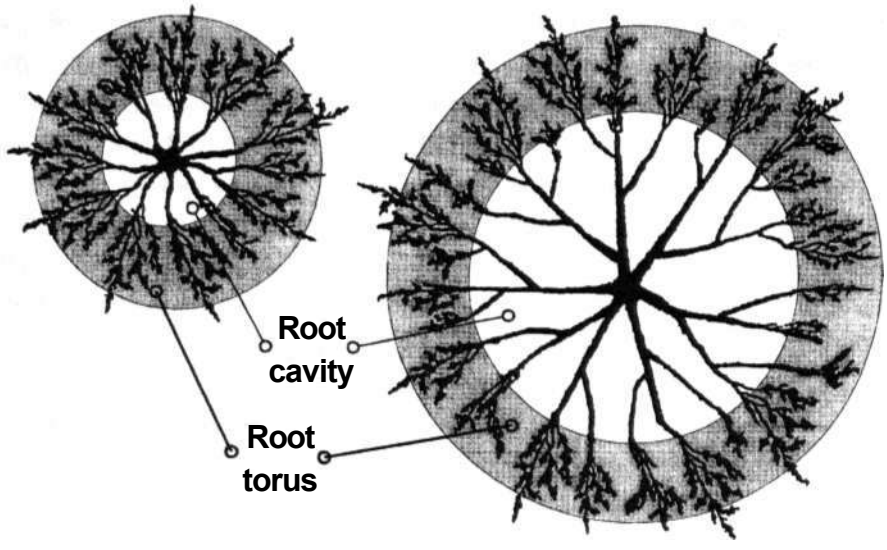


Fig. 8. The search for new territories determines the formation of a peripheral torus of absorbing rootlets. The distance of the torus from the trunk increases with age.

absorbing periphery will therefore be defined as the root torus*, and differentiated from skeleton roots that reach the trunk passing through a barren cavity. Root cavitation lasts for the plant's life in orchards, in spite of the rapid nutrient re-equilibrium. The recovery is proven by chemical analyses, and by the fertility of the cavity for "compatible" foreign species observed in cenosis (Section 3.3).

Autophobia and centrifugal stride also explain the deepening of the root system with plant aging, as root renovation is reduced at this stage, becoming unable to compensate for die-back losses. This leads the Root to restrict its territory, and to deepen the absorbing apparatus (Zucconi 1988), which may withstand anaerobiosis better than dyspathy (Fig. 9). The allocation of the torus itself changes through such evolution, being affected by plant age and its regenerative power.

An indirect way of visualizing the impact of autophobia on centrifugity comes, again, from hydroponics. Predictably, Root cavitation does not occur here, because root die-back is reduced to a minimum and soluble excretions or metabolites are washed away with solution changes. The result is an expanding Root that keeps its absorbing roots almost intact. This adds to the dynamics of centrifugity, and accounts for its variability when changing environments. Finally, in conditions of high soil leaching (e.g., the rain forest) the root may reside longer in a territory due to the elution of secondary allelopathic factors.

Root *macromigration**

The sharing of niches

A plant-inhabited soil is compartmentalized in separate *niches*, which represent discrete portions of the territory, each used by a single root. Other roots are precluded from

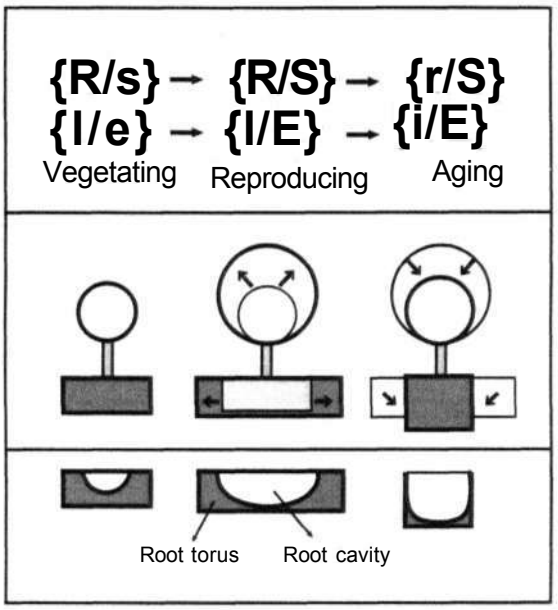


Fig. 9. Root system spread (depth and width), and its relation to plant life stages. The root system deepens with age, also changing its torus distribution.

entering into an occupied niche by the presence of excretions produced by the resident Root. These excretions are primary allelopathic factors, or PAFs, and serve a number of purposes: (1) they ameliorate the soil; (2) favor absorption; and (3) select a favorable rhizosphere (Neal et al. 1970). More relevant for this analysis, (4) they "mark" the territory (Zucconi 1993), and make its use exclusive by revealing the presence of the resident root. The result of such demarcation is both to avoid an indiscriminate overlapping of roots from same or different plants in a single territory, and to allow the root to undergo a residential phase of nutritional exploitation of the niche.

The existence of PAFs then represents a cardinal feature in biomic organization, by regulating the share of soil among roots and between plants. It also maximizes the efficiency of soil usage by each of them, at anyone time, and by the cenosis on the long run. The PAFs also bear a fundamental role in organizing the geometry of the root systems. In particular, they impose precise distances between scaffold roots, acting as "external" correlative factors in regulating their radial and planar distribution.

The advantage of soil compartmentation, however, is temporary, because it also checks the micromigration at the boundary of neighboring niches. The plant then solves its urge for finding additional substrate (Fig. 10) by forming transmigratory roots. These are thick roots that undergo flushes of extended growth (macromigration, or *transmigration** from Zucconi 1993), that allows them to cross the territories of other roots in the search of available niches. Absorption is precluded in these roots, although it may be resumed by their laterals when arriving at a compatible substrate. Contrary to the appearance, niche markers are not simply inhibiting factors, as transmigratory roots use them to identify the shortest way to unused (unmarked) territories.

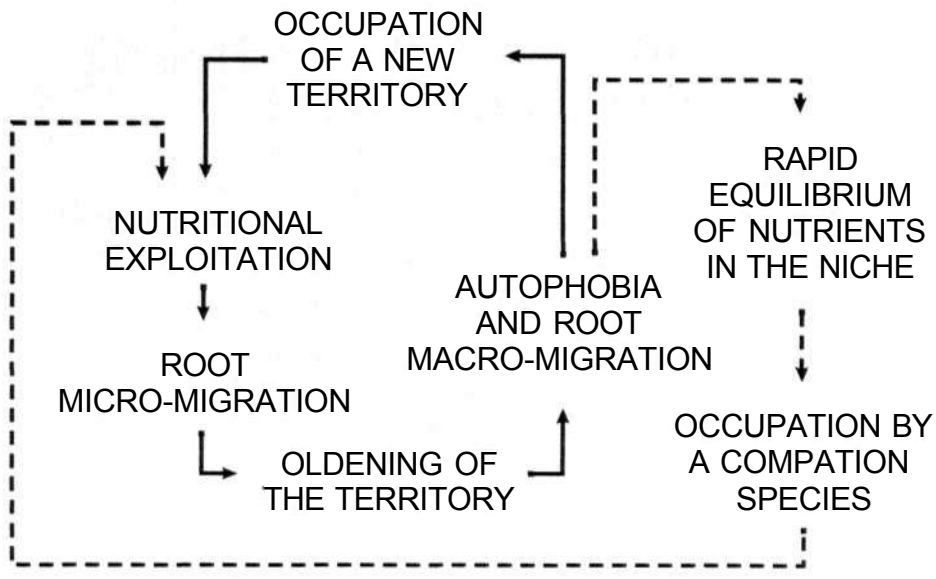


Fig. 10. Roots undergo a perpetual transmigration in the quest for fresh territories. These territories become "old" and are abandoned when laden with root residues. The abandoned territories are not depleted nutritionally, and may be reused by compatible foreign species.

Macromigration, although representing a basic mechanism in Root formation, prevails in young plants, thus accounting for the their high territorial competitiveness and for the decrease of such a competitiveness with aging (Fig. 9). Life in cenosis delays such evolution in proportion to the occurrence of niche rotation between species (following section). Agricultural plants in monophytic stands lack a comparable soil sharing so that the arrest of the Root expansion occurs earlier, while they soon lose their juvenile stride. This arrest is particularly precocious when such plants are genetically manipulated, or vegetatively propagated. It follows a variable pattern of root distribution which, to be understood, requires the preliminary analysis of niche sharing between species.

Interspecific compatibility

As an abandoned niche reacquires its mineral fertility, it is coveted by the roots of different species, among those "compatible" with the residing residues (Fig. 10). Actually, the co-existence of self-incompatibility (autophobia) and interspecific compatibility *(eupathy** or xenophily) causes a reiteration of the niche use-abandon process, leading to an alternation of species, no one of which may station indefinitely in it. Compatibility in the sequential use of a niche, on the other hand, does not represent a reciprocal feature among any two species, but rather a property shared between a restricted number of species, and often only in a given sequence (Zucconi 1993). This accounts for the specific diverse retinues *(cortege*)* that characterize individual phytocenoses. The sequence of species in a soil niche follows a compatibility hierarchy with the latest resident(s); each new species masking the mark of the former(s) by its own residues, thus also shifting the access hierarchy for other species. The compatibility hierarchy is not the only factor determining such a sequence, however;

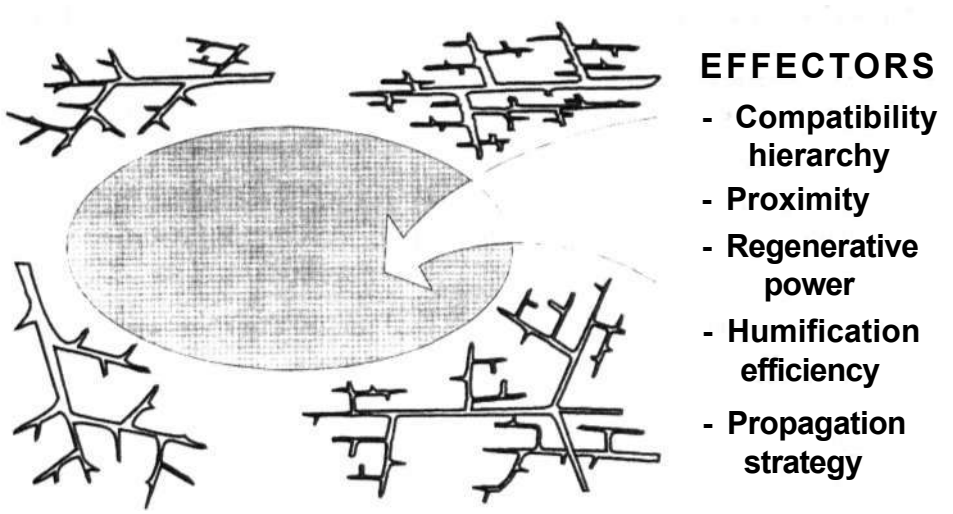


Fig. 11. Factors affecting the hierarchy in the occupation of an abandoned niche.

other factors being root proximity, regenerative strive (higher in young plants), and seed dissemination strategies (Fig. 11).

The sequential niche use by species in cortege amounts to a root *rotation**,* with peculiar effects on the organization of plants and communities. Among these, it is the cyclic return of any one species, when itself becomes compatible with the latest resident(s). Such a return is proportionally faster with the onset of humification, by far the quickest stabilizing process, at our latitude, and capable of transforming specific residues into a new type of organic aggregate endowed with a greater interspecific compatibility (Zucconi 1988, 1993). A new factor may then account for the compatibility between species in cortege, i.e., the interactivity in the stabilization of their combined residues *{co-humification** from Zucconi 1983,1991; Zucconi and de Bertoldi 1987).

From a biomic organization viewpoint, the renovation of the niche by a sequence of compatible species allows each plant to profit from the cyclic availability of "fresh" territories, existing at Root reach. The Root, then, does not have to extend indefinitely from the stem to restore its absorption process. This condition increases the potential plant longevity in cenosis, where it requires a modest energy investment for maintaining a vital root renovation. Opposite to this, a low absorption efficiency develops with monocropping, which is favorably redressed by crop rotation or intercropping.

A major point in this analysis is that allelopathies are not depicted as hampering the root through the presence of toxins and often implied in literature (Rice 1974; Putnam and Tang 1986). On the contrary, primary and secondary allelopatic factors are seen as responsible for (a) the autonomous organization of plants and communities, (b) the coordination in the root distribution (Fig. 12), (c) the efficiency in soil sharing between plants, and (d) the equilibrium of species in cenoses. The synoptic view of these events in

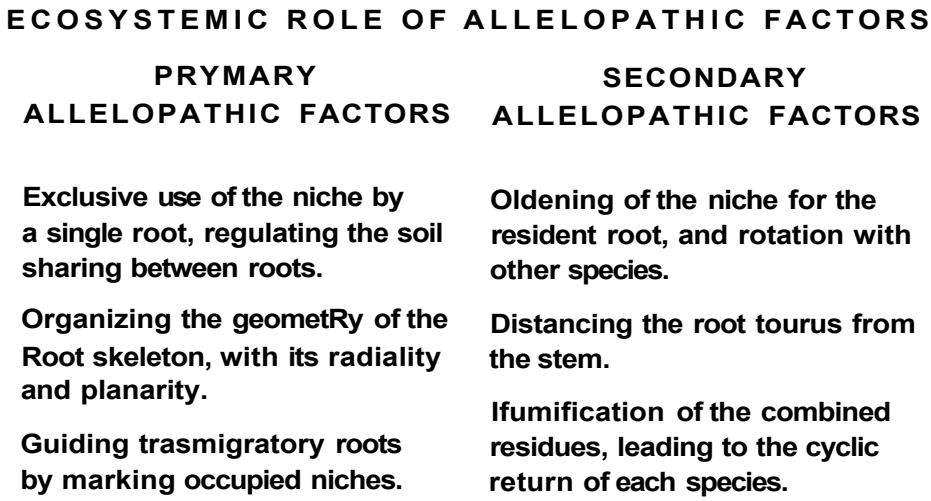


Fig. 12. Ecosystemic role of primary and secondary factors in the organization of root development and soil sharing between plants.

Figure 12 illustrates the multiformity of PAF and SAF actions, thus vesting allelopathies with a fundamental role in the organization of the ecosystems (Zucconi 1991). Indeed, the root is an unrenunciable interpreter of the interaction between plants, and it does so (a) by producing, directly or indirectly, allelopathic factors, and (b) by sensing their presence and quality.

The setting of phytocoenoses

At the phytocenotic level, the existence of dyspathies and eupathies generates a dipole (Fig. 13) in which opposite forces sort the plants based on their different allelopathic stand (Zucconi 1993). In doing so, the dipole provides a selective advantage for attracting compatible foreign species to a close stand (cortege), and for setting apart both plants from the same species (peers), and foreign incompatible plants *(xenophobia*).* The compatibility hierarchy then represents another facet of the allelopathic organization, and in fact accounts for its driving force. At the same time, the distance among peer plants in cenosis is determined by the need to create a buffer zone in which a sequence of different species reinstores a given plant in a privileged status, raising the probability of its presence.

The allelopathic equilibrium shown in Figure 13 also justifies the effectiveness of crop rotations in agriculture; its success deriving from the ability to mimic the natural alternation of roots from different species, and the combination of their residues. Thus, in a condition in which phytodiversity is precluded on a coeval stand, the species succession brought by rotation reinstalls some of the ecological equilibria that characterize the organization of cenosis.

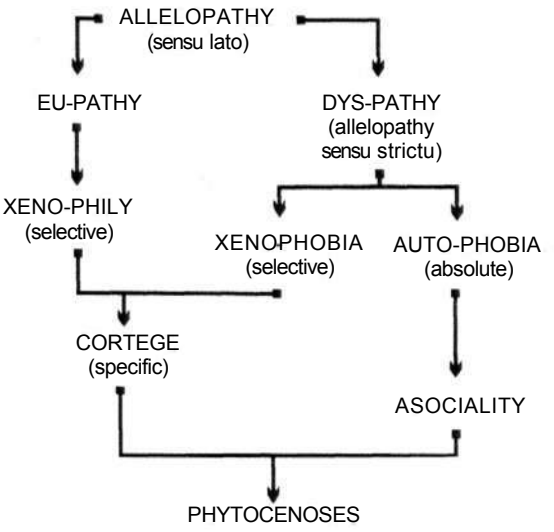
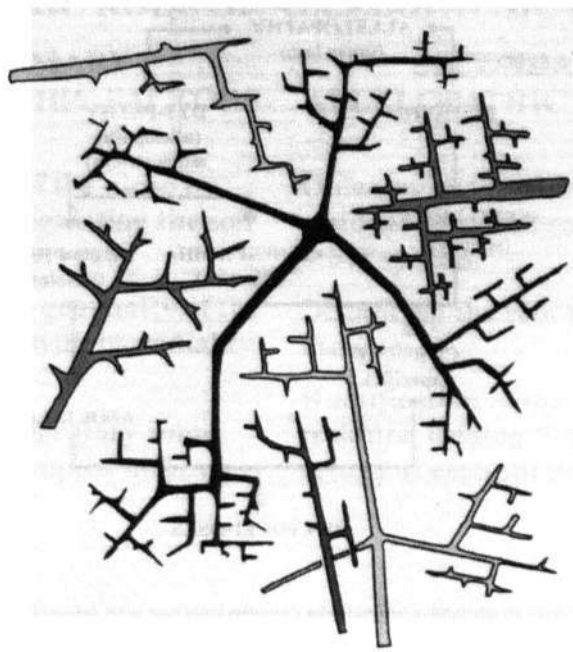


Fig. 13. Opposite allelopathic forces attract compatible foreign species and separate plants from the same species, accounting for the mixed stand existing in phytocoenoses.

The distribution of root systems

The allelopathic behavior of roots in the cohabitation of plants from the same or different species, as existing respectively in agricultural or in natural stands, leads to the formation of two basic types of spatial Root distribution. With perennial plants in cenosis, the existence of a mixed vegetation determines the spread of a Root in separate areas of a territory, intermixing with the root of other species (Fig. 14). The existence of such a dispersed Root torus eases the soil turnover among species, thus avoiding root cavitation and soil waste (Zucconi 1991). In fruit orchards, where the borders of the allelopathic pot are rigidly set by the contiguity of peer plants, Roots do not cross the boundaries of neighboring trees (Fig. 7), and therefore remain confined as if in a physical container (Fig. 15). The lowering of the root transmigratory urge contributes to such a confinement, providing a different model of Root distribution and implying a different physiological behavior.

A peculiar Root distribution, and in many respects a simpler one, characterizes most annual species. These maximize the advantages of their ephemeral stand by following one another in a niche, along a cyclic seasonal succession. A Root of this type uses a single niche that it exploits for its entire (short) life, and which it may reoccupy in the next generation, depending on its compatibility with the interposed residents. It follows a niche rotation process that implicates entire plants in their seasonal ephemeral stand. Rotation of such species then supports a cyclic change of vegetal scenarios, thus giving rise to *pulsative cenoses*.* Although such behavior does not apply to all herbaceous plants, it includes the gramineae, which we analyze in Section 6.1.



Fig, 14. The Root of a woody species in a mixed cenotic stand spreads satellite subsystems between the territories of different species. The result is a fragmented torus intermixed with those of foreign species.

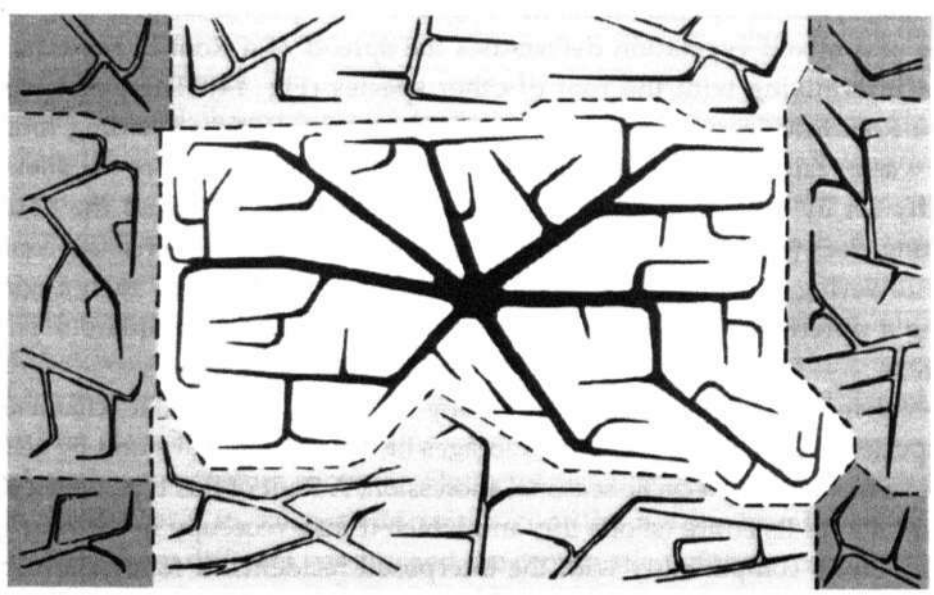


Fig. 15. The Root of a fruit tree in a monospecific orchard remains confined within the allelopathic pot created by adjacent root systems.

Allelopathy and the agricultural ecosystem

Vegetative-reproductive strategies in cultivated plants

The soil volume used by a cultivated plant undergoes a progressive cavitation, with the Root torus expanding in the available territory up to the boundary of neighboring Roots. Here it gets to an arrest (Fig. 15), being neither able to progress, due to the presence of PAFs, nor to regress, due to SAFs. When the arrest (stillness) occurs at an advanced young stage, the R/S ratio tends to slide towards the critical mass, with the Root losing its urge to expand and reaching a stand still. The result is a Root confinement in an allelopathic pot, where the trophic use of the substrate is limited to a peripheral layer, thus also reducing the ipogean (1) factor.

The plant sliding towards the critical mass shows a rapid reduction of the R/S ratio because, in this condition, the Shoot experiences a residual growth. At the same time, the Root lowers its demand for the E factor and reduces its 1 factor production. These conditions then contribute to lower the I/E ratio in the Shoot ({i/E}), compelling a homeorhetic switch from a vegetative to a reproductive stage (Fig. 5). In comparison, natural species of analogous physiological age would react differently to a restricted space by forming transmigratory roots and scouting strenuously for further substrate.

The agricultural plant, however, interprets the arrest of the Root at the boundary of the allelopathic pot as a signal for timing its transition to reproductivity, and the plant uses its flexibility to adapt its size and physiology to the substrate availability and to Root expansion (Fig. 4). Within certain limits, then, cultivated plants may be increasingly dwarfed and brought to an earlier reproductive stand in response to planting density. This differs again from the behavior of natural species in which the root transmigratory urge would maintain a high root vegetative strive and delay plant maturity.

The homeorhetic switch to maturity is stable in polycarpic plants in which the onset of Root stillness allows the switch to a reproductive homeostasis (Fig. 16, right), and this is maintained by the fruit competitive use of the epigean (E) factor. Starvation of the Root follows because the Root itself is a loser in this *compensative correlation** due to its greater remoteness from the source (Zimmermann and Brown 1971), when compared to the fruit. Root starvation is followed by a lower activity (and a reduced E-factor request), with a consequential low availability of the I-factor for the shoots. The result is to create a permanent low {i/E} ratio in the Shoot, a condition that favors the perpetuation of reproduction. The differential Root dynamism, before or after encountering the boundaries of the allelopatic pot, then represents a fundamental regulatory mechanism in the development of agricultural plants. It amounts to an evolution from a vegetative to a reproductive equilibrium, or vegetative-reproductive homeorhesis (Fig. 16), a process which is completed in a few seasons in fruit trees, and in a few weeks in grasses.

As a result of an earlier fruiting, the plant invests less energy in vegetative growth and organ renovation, and remains small; this feature is exploited by fruit growers who resort to reduced spaces in order to dwarf fruit trees and hasten their reproductivity. Breeders seek analogous advantages by devising a programmed space for the sowing of grain crops.

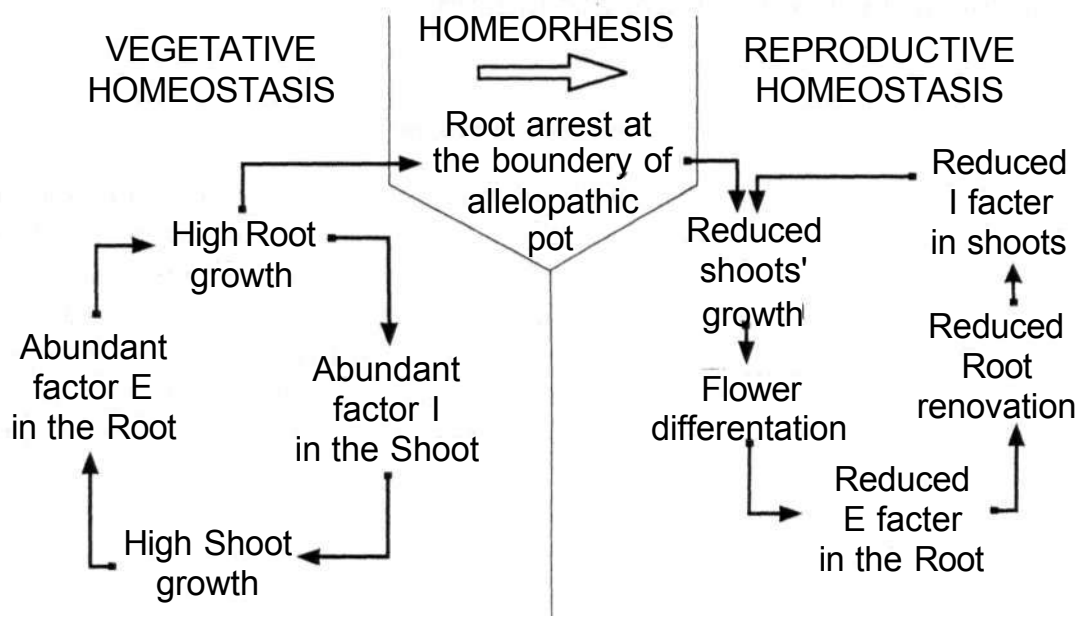


Fig. 16. The arrest of the root system in an allelopathic pot, in cropped plants, allows the homeoretic shift from vegetative to reproductive homeostasis.

Such crops, then, also benefit from uniform spacing for synchronizing maturation. Finally, the reduction of root and shoot renovation caused by fruiting shortens the plant life cycle, thus hastening maturation in annual crops. It reduces considerably the fruit tree life, however, compelling the growers to resort to rejuvenation practices by the use of pruning and fertilizers.

Adaptation to a reduced substrate volume is also part of some specific strategies in nature, where it has favored the evolution of annual plants. Such plants have renounced a durable structure in favor of an opportunistic approach to a short life cycle and an early fruiting. Many such species, and the gramineae in particular, maintain a flexible relation to space, i.e., they grow a smaller Root and a simple stem when confined in a reduced volume, or an enlarged Root and a branched Shoot when provided with a greater space. It is not by chance that agriculture began from these species, by exploiting their adaptability to thrive in the reduced space allotted by the allelopathic pot in monophytic cropping.

Selective impact of agriculture on plant adaptation

The agriculture production standards, by the raising of plants in monophytic crops, confronts the root with the accumulation of monogenic residues* (i.e., from a single biological source) in the soil. This accumulation reduces the saprophytic diversity, which debases humification to the advantage of toxicogenic degradations. Such degradations, in turn, have dystrophic effects on the root (Zucconi 1983, 1993; Zucconi and Monaco 1987) which may now experience an increasing difficulty in absorbing nutrients and water, and may even die. Toxicogenic degradations also debase the rhizospheric organization, with an

expansion of opportunistic organisms, including biotrophs. This process, albeit foreseeable, has commanded scarce attention as to its real mechanism, in spite of being a strong signal of ecosystemic degradation.

Indeed, conditions set by forced cohabitation and accumulation of monogenic residues are hardly compatible with the vast majority of natural plants, that would react by forming transmigratory roots and scouting for "fresh" substrates. A similar strategy, however, would be detrimental in monophytic stands, where it would commit the Root to an energy-exhausting search for improbable niches of fresh soil. This would stunt Shoot growth, and lead to nutrient deficiencies and senescence (as known in woody plant nurseries).

In conclusion, whereas mixed stands select species more sensitive to the impact of xenophily and autophobia (Fig. 13), monophytic cohabitation in agriculture brings a selective pressure towards reducing the Root expansion effort, and in turn requiring an increased *self-tolerance** (Fig. 17). In this condition, the Root tends towards a residentiality that allows it to withstand cohabitation with peer plants. This behavior, defined as *sociability** (as opposed to the cortege of natural plants), derives from the ability to withstand a substrate reduction by shifting the available energies towards reproduction. This behavior allows to predict the existence of a smaller Root in cultivated than in wild varieties, and a shorter juvenile stand (Fig. 18). This model is confirmed by the findings of Iwama and Nishibe (1989), i.e., a lower root/leaf ratio in cultivated versus wild potato varieties. The change towards a greater residentiality in cultivated plants is particularly pronounced in genetically improved varieties (mainly gramineae) selected for dense stands and repeated cropping.

Another aspect of the accumulation of monogenic residues is the onset of anomalous metabolism, i.e., toxic to root absorption and to the rhizosphere (Zucconi 1993). Therefore, agricultural plants have also adapted to withstand such toxins (Zucconi 1991, Neri et al. 1996), possibly through the reduction in autopathic sensitivity (Figs. 17,19). The plant must have also assumed a greater trophic autonomy in the presence of a reduced rhizosphere, and thus increased its capability to absorb mineral nutrients (Fig. 19). Actually, such a task is compensated for by the reduced competition for the substrate existing in agriculture, and by irrigation and fertilization practices; an aptitude by now extensively exploited in the genetic selection of gramineae.

In conclusion, the high sociability of agricultural plants is the inevitable, as well as inadvertent, result of the selective pressure exerted by the domestication process. In this case, plants characterized by Root residentiality were rapidly favored due to their greater proclivity to withdraw from growing and to reproduce, thus also undergoing a further evolution. In the same populations, more autophobic plants are bound to undergo an exhaustive root transmigration, becoming less competitive for reproduction and experiencing a self-elimination. Changes towards sociability are hardly extreme, however, considering the evolution of gramineae. Furthermore, life colonization of the land has required adaptations to new and variable conditions, often more complex than those occurring in the agricultural ecosystem.

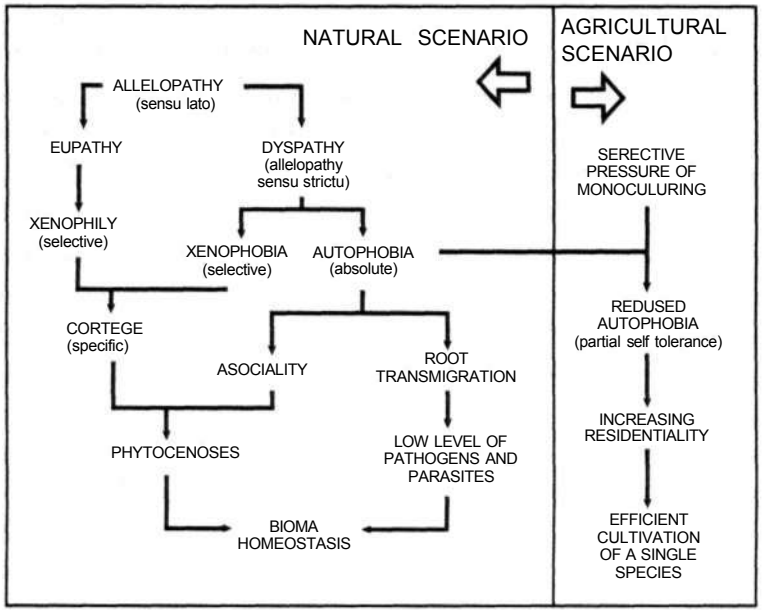


Fig. 17. The mechanism of autophobia and root migration in natural plants is lost in agriculture, where plants are subjected to the selective pressure of cohabitation resulting in an adaptation towards self-compatibility and residentiality.

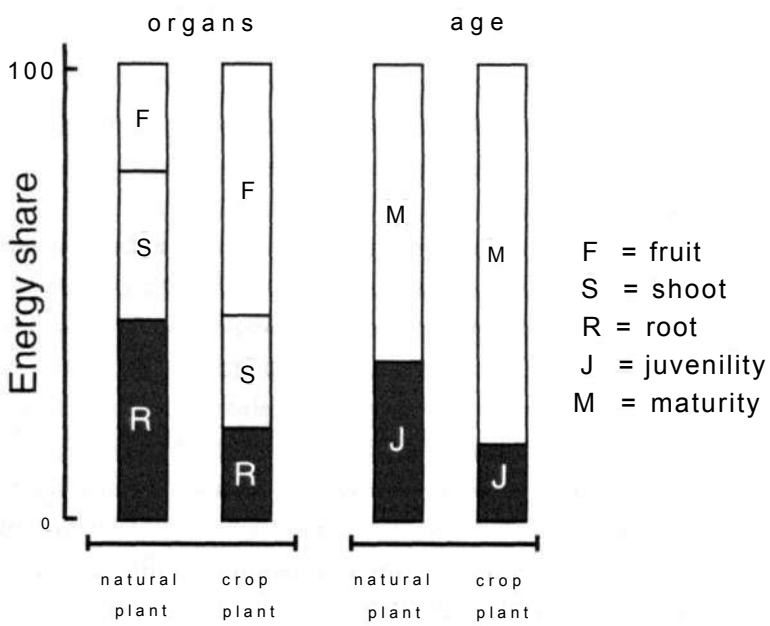


Fig. 18. The agriculture phytotype is characterized by a greater energy share to fruiting.

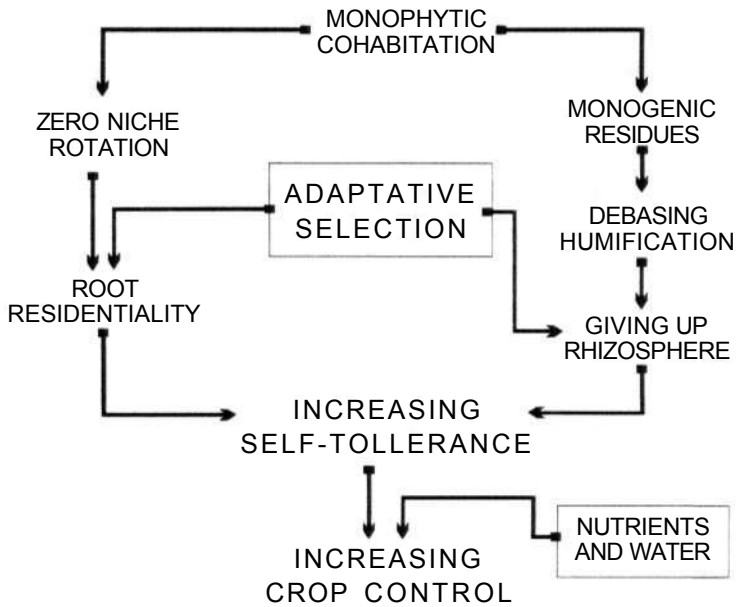


Fig. 19. Monophytic cohabitation alters the environment and causes adaptive changes in the plant, leading to greater self-tolerance.

Agriculture and civilization: input and feedback

Advantages of plant sociality

The selection towards an increasing self-tolerance favored the formation of "new" plants characterized by a small, residential Root, less engaged in growth, and less demanding in energy. More E factor can then be retained in the Shoot. Here it is used less by growth, limited by the scarcity of the I-factor, while it increases the share allotted to reproduction ({i/E(:Zucconi 1994 a,b).

Root residentiality, and the increased self-tolerance that makes it possible, then has inadvertedly created an adapted plant to the agricultural environment, providing a powerful tool for selection. This plant represents a winning model also in genetic programs that have selected grain crops by screening in conditions of high density and liberal supply of fertilizers. Most successful species that pass this screening belong to the gramineae, confirming their greater adaptive potential for residentiality. Indeed it is not by chance that these species were the first to be brought to cultivation, accounting for the rise of a number of independent civilizations. This conclusion reflects the history of barley and wheat in Asia Minor (from the 10th millennium b. c. e. - before the common era), and their expansion to the Euphrates (Ofeid civilization, 6th millennium b. c. e.), and to the Nile valley and Europe (5th millennium b.c.e.). It also reflects the history of rice in East-Asia,

spreading from inner China (high Hebei and Shanxi regions, 4th millennium b.c.e.), and of corn in Central America (1st millennium b.c.e.).

In conclusion, the overall result of monophytic cultivation is the evolution towards an agricultural phytotype, characterized by (a) the loss of the Root transmigratory urge, (b) an acquired self-tolerance (Figs. 17, 19), and (c) the reorganization in the use of energies in favor of the reproductive process (Fig. 18). Along this evolution, the allelopatic pot constriction of the Root and the deterioration of humification have progressively eroded the plant command of its trophism, demanding compensative supplies of water and nutrients (Fig. 19). It may be observed that the development of writing (an administrative tool created in Sumer for recording stored agriculture products: about 3.500-3.200 b.c.e.) paralleled the development of advanced channeling and irrigation engineering, which resulted in a greater control of productivity. The husbandry of fertilization, starting with organic amending (still cherished in China) up to the recent use of mineral fertilization, also contributed to this productivity control.

An unfinished work

The selection of self-tolerance and residentiality in cultivated ecosystems favors the confinement of the individual plant in the allelopathic pot. Missing benefits of cenosis, this adaptation results from a progressive selection to withstand both a lower degree of cooperation with rhizospheric organisms and a greater reliance on a direct mineral absorption. Consequences go beyond the trophic sphere as the reduction of saprophytes and humification leads to a compensatory expansion of biothrophes (Zucconi 1991), many of which, such as pathogens and parasites, have today become a major problem in agricultural production. Biotrophes are now able to expand in proportion to the

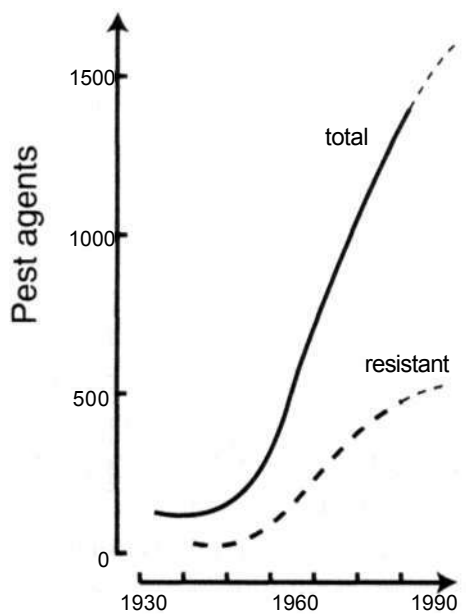


Fig. 20. An estimation of the increase in disease agents during this century in Italy ("total" line), including that of pesticide resistant ones ("resistant" line). (Adapted from Tremblay 1990).

monoculturing extension. Also their expansion was amplified, in the last two generations, by the saprophyte-suppressive impact of pesticides and fertilizers, and to an acquired resistance to pesticides (Fig. 20). Being undeterred in proportion to the debasement of biomic organization, they may now expand to previously unknown virulence levels.

This leads to the conclusion that the selection towards an agricultural phytoptype, for many aspects successful, has possibly been stretched to its utmost capability for adapting to sociability and ecosystemic degradation; and any further pressure along this line might easily lead to a rapid loss in cultivative efficiency. Past agriculture resorted to species variation while confining monophytism to small plots frequently rotated, often within the year. Compared to this, the actual insistence on fewer extensive crops, the erosion of rotations, and the increase in genetic standardization are possibly already beyond any acceptable minimum equilibrium. Thus it may lead to a loss of sustainability and put the endurance of the cultivative model at risk. All this places some serious doubts on a production strategy that takes in no account factors involving ecosystemic organization, and that has already exhausted them to the utmost (Zucconi 1991), with little margin for further exploitation.

Glossary

Glossary of new or redefined words from the present article. Asterisks (*) mark words defined in other parts of the glossary.

Agricultural phytotype: plant adapted, through a progressive selection, to perform efficiently in the specific environmental conditions set by cultivation practices.

Allelopathic pot: space allotted to the root system (Root) by the boundaries of other Roots, and opposing its quest for expansion.

Allelopathy: reciprocal acceptance or repulsion in association (Root contiguity), and manifested through autopathy*, xenophobia*, and xenophily*. The current use of the term in a negative sense (suffering) is too restrictive in comparison to the ecophysiological action of allelopathies, and inconsistent with etymology.

Autophobia: dyspathy* for the own residues.

Bioma: ensemble of living organisms in their mass, differentiation of species, and cenotic* association.

Cavitation (root): the loss of absorbing rootlets, within the core of a Root. Rootlets expand at the periphery forming a root torus*.

Cenosis: cooperative association between integrated species, implying closeness of foreign organisms and remoteness of peer ones.

Centrifugity (root): tendency of roots to absorb in ever new soil, expanding peripherally.

Co-humification: stabilization through humification as influenced by the combined residues from different origins (poligenic residues*).

Compensative correlation: competition of organs for a common substrate.

Cortege: different species courting a single species, and isolating it from its peers, according to specific xenophilic* interactions.

Critical mass: level of I/E or R/S ratios above which the plant vegetates and below which it turns to reproduction.

Cybernetics: science that studies regulation at its "decisional" level.

Domestication: the process of plant adaptation to cultivative environments, allowing them to achieve a high production potential (agriculture phytotype*).

Dyspathy: repulsion or sufferance in the encounter between roots or with their residues. Opposite to eupathy*.

Dystrophy: inability to properly nourish oneself due to the impact of dyspathies*.

Edaphic correlation: concurrence of different plant organs in the making of a common substrate.

Effectors: factors and conditions.

Epigenesis: the plant discriminative expression of its genetic potential.

Epigean factor (above-ground factor, E factor): the exclusive or preferential product of Shoot activity necessary to Root and Shoot. It exerts a limiting function on the vegetative growth of the Root that does not generate it.

Eupathy: attraction and interaction in the encounter between different roots. The opposite is dyspathy*.

Homeorhesis: gradual homogeneous evolution between homeostatic* equilibria.

Homeostasis: capability of maintaining in constant the internal conditions of a system.

Ipogean factor (below-ground factor, I factor): the exclusive or preferential product of Root activity necessary to Root and Shoot. It exerts a limiting role on the vegetative growth of the Shoot that does not generate it.

Macromigration: fast extended growth of exploratory roots which cross the niches* of other roots, without absorbing, in the search for empty territories.

Micromigration: slow, continuous creeping of absorbing rootlets beyond the range of the nutritionally exploited substrate.

Migration: opposite of transmigration*; see also micromigration*.

Monogenic residues: organic residues from a single biological origin.

Niche: discrete portion of soil nutritionally used by a single root, and shared in rotation* between roots of different species.

Oldening (soil): growing root autopathy* for absorbing within its niche that is increasingly laden with its own residues.

PAFs: see primary allelopathic factors.

Primary allelopathic factors (PAFs): allelochemicals actively excreted by the root to mark its territory.

Pulsative cenoses: annual species that follow each other in the soil, in transient seasonal cenoses.

Residentiality (root): a phase in root development coinciding with absorption in its own marked niche*, lasting until saturation with its root residues. The increased residentiality of agricultural plants is accompanied by a lower dyspathy for the own teritory (oikophobia*).

Rotation (root): sequential use of a single soil niche* by the roots of single compatible species, each using the niche temporarily.

SAFs: see secondary allelopathic factors.

Secondary allelopathic factors (SAFs): metabolites from the microbial decomposition of organic residues. PAFs exert a strong autophobic* effect on the plant that produced the residues.

Self-tolerance: condition of reduction of autopathy*

Sociability: acceptance of a close standing of peer plants without transmigrating the Root (residentiality*).

System: integrated ensemble characterized by the interaction of the functions of its parts.

Torus (root): absorbing periphery of a Root, surrounding the internal cavitation*

Transmigration: opposite to migration or macromigration*.

Trophism: ability to satisfy the nutrient demand.

Xenophily: eupathy* towards foreign plants (different species).

Xenophobia: dyspathy* for the residues of foreign species.

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Spatial Distribution of Root Systems and Root Activities

P. J. Gregory[1]

Abstract

Generally, the increase in size of the root system of annual crops, such as wheat and lupin, can be characterized by an expolinear equation. For determinate, annual crops, little assimilate appears to be allocated to the roots once flowering has occurred, although in indeterminate species (e.g., chickpea) the root system may continue to expand during seed filling. The exact amount of carbon translocated below ground is a matter of speculation because the turnover of roots and loss of carbon by exudation has rarely been measured infield conditions; estimates range from <5% to 40% of fixed carbon.

After the initial phase of growth, rooting depth appears to increase linearly with time until the final depth is reached. There is currently no theoretical basis for defining root depth, but the vertical distribution of root length can often be described by a simple exponential decrease in length with depth. Hard layers, marked textural changes between horizons, and localized concentrations of nutrients (particularly nitrate) can perturb this distribution.

Water uptake by a growing root system can be described by two functions that define the downward extent of the extraction front and extraction behavior of the roots. Although these functions are physically based and give an adequate description of parts of the activity of lupin and wheat root systems, some anomalies in behavior remain unresolved.

Introduction

In most crops, roots are the organs that absorb nearly all of the water and nutrients taken up. They are sites of production for chemicals that maintain root:shoot integrity and also provide anchorage so that the shoot can expand leaf area to capture radiation without the plant toppling. It is now well recognized that the growth of root and shoot systems is an integrated process in which homeostasis is maintained as a consequence of both the size and activity of the two systems (Davidson, 1969; Hunt et al. 1990).

This chapter reviews some common features of the growth of root systems as deduced from a wide range of field studies and illustrates some of the main points with results

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obtained from wheat and lupin crops grown in Western Australia. In addition to these crops grown on shallow, duplex (about 30 cm sand overlying deeply weathered kaolinitic clay) soils in a mediterranean climate, results from barley crops grown on inceptisols in northern Syria will be used to highlight relations between growth and temporal patterns of water uptake.

Dynamics of root growth

Because roots are difficult to measure, but shoots have readily identifiable stages of development in most cereal crops, there have been long-standing attempts to quantify the interaction between shoot and root development. In cereals, root axes arise from both primordia in the seed (seminal axes) and at the base of the leaves (nodal, crown, or adventitious axes). The number of seminal axes varies between species (typically 7-8 in barley, 5-6 in wheat, and 1 in millet and maize) and are usually all expressed, whereas the number of nodal axes appearing is often limited by adverse environments (Troughton 1980; Gregory 1987). Klepper et al. (1984) developed a systematic identification scheme for root axes of wheat *(Triticum aestivum)* and then related the appearance of axes to that of leaves and tillers. They found that the number of nodal axes (R_n) on any culm was linearly related to the number of leaves (L_n) on the culm by $R_n = 1.95\ L_n - 3.06$. Similarly, Gregory (1983) also found a linear relation for root axes of pearl millet *(Pennisetum typhoides* S. & H.) of $R_n = 1.42\ L_n - 2.26$. In many studies, it has been found that the time interval between the appearance of leaves is approximately constant and proportional to the thermal time (in °Cd) that has elapsed [about 110 °Cd for wheat (Avalon), and 25 °Cd for pearl millet (BK 560)]. Such relations describe the potential production of axes well although the actual production depends on environmental conditions, particularly the surface water content for the production of nodal axes (Gregory 1987) and radiation and nutrition for the production of tillers (Vincent and Gregory 1989) and their accompanying nodal axes.

Dry matter accumulation by root systems typically follows the sigmoidal pattern commonly observed with shoots (Fig. 1). In cereals, flowering appears as a particularly important developmental stage after which assimilates are required predominantly to fill the growing grain, leaving little assimilate for roots (Keith et al. 1986; Gregory and Atwell 1991). In most cereals, the mass of the root system rarely increases after flowering and may decrease substantially depending on soil conditions. For legumes, the situation is less certain. Figure 1 shows continued increase in the length of the chickpea root system during early grain-filling (Brown et al. 1989), a result also obtained by Sivakumar et al. (1977) with soybean and by Gregory and Eastham (1996) with lupin. However, the degree of determinancy may influence the pattern of carbohydrate allocation to the root system (Mayaki et al. 1976).

Goudriaan and Monteith (1990) demonstrated that the growth of crop stands in light-limited conditions could be described by the equation

$$W = (C_m/R_m)\ln\{1 + \exp[R_m(t-t_b)]\} \quad (1)$$

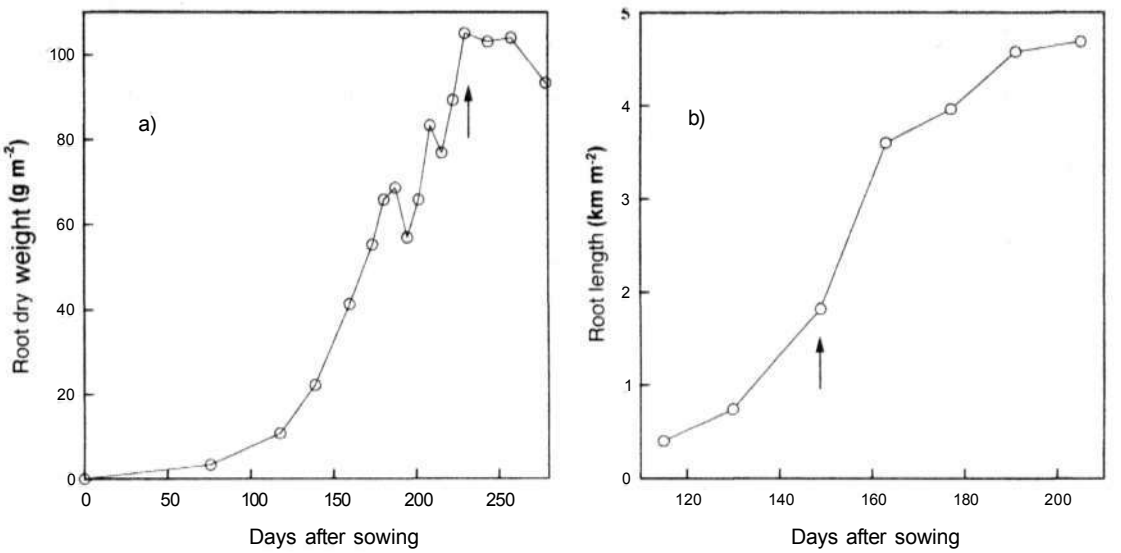
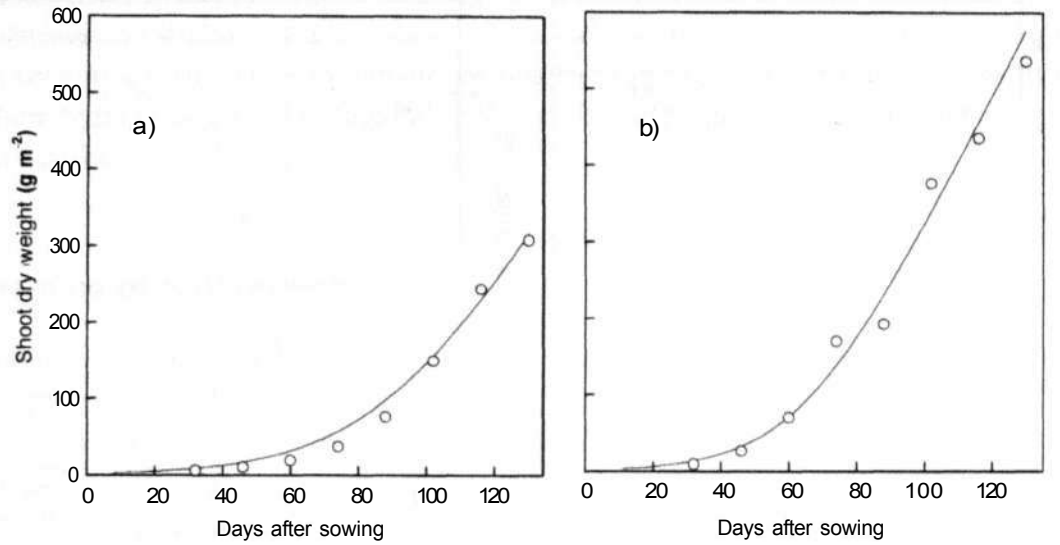


Fig. 1. Changes during the growing season in (a) root dry weight of wheat (from Gregory et al. 1978), and (b) root length of chickpea (from Brown et al. 1989). The time of flowering is shown with an arrow.

where W is the dry weight of the crop, C_m is the maximum rate of crop growth, R_m is the maximum relative crop growth rate, t is time, and t_b is the "lost time" (Monteith 1981) determining the position of the curve on the time axis. They termed this "expolinear" growth, and showed that it gave a good fit to experimental data for shoot growth of crops of sorghum, faba bean, and oil palm (Goudriaan and Monteith, 1990). The equation is based on a few simple assumptions. First, that the fraction of radiation intercepted by a canopy can be described by Beer's Law with a constant extinction coefficient. Second, that the rate of crop growth is directly proportional to the fraction of radiation intercepted. Finally, that there is a constant ratio between leaf area and shoot dry matter. The last is the weakest assumption [see Goudriaan (1994) for discussion]. In principle, there is no reason why the same analysis should not be applied to root growth, provided that the specific root weight remains constant with time. Figure 2 shows that equation 1 provides a good fit to the measurements of shoot growth obtained for lupin and wheat crops grown in Western Australia [see Gregory and Eastham (1996) for details]. Both crops were sown as early as possible after the winter rains commenced and both crops were given moderate amounts of phosphorus (P) and potassium (K) fertilizers although only the wheat was given nitrogen (N). The parameter values (Table 1) were found by separate linear regressions of the estimated exponential and linear growth phases as calculated by Gregory and Eastham (1996). A similar analysis applied to the root systems also gave good agreement with the experimental measurements despite the uncertainty as to whether or not light was the only limiting factor in the growth of these crops (Fig. 3).

Most estimates of root biomass, including those in Figures 1 and 3, are obtained by soil coring followed by extraction of the roots by washing with water. This gives a measure only of the balance between new roots produced and older roots that have senesced, so that the actual production of root biomass is often uncertain (Huck et al. 1987). Moreover, during washing and storage, substantial amounts of fine roots and soluble carbohydrates



Fig, 2. Fit of the expolinear equation (line) to shoot dry weight (O measured) of (a) lupin and (b) wheat crops grown at East Beverley, Western Australia in 1991

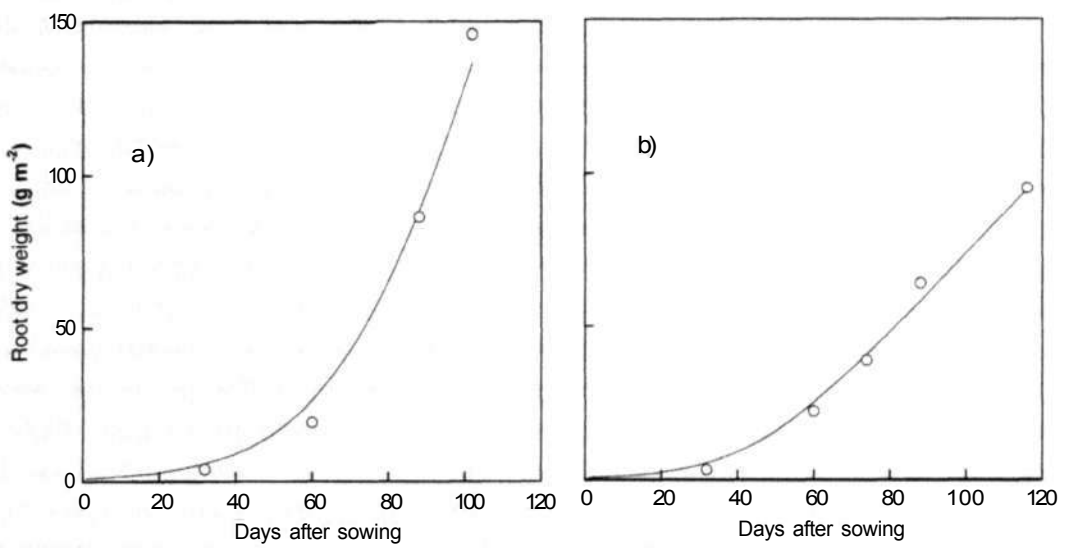


Fig. 3. Fit of the expolinear equation (line) to root dry weight (O measured) of (a) lupin and (b) wheat crops grown at East Beverley, Western Australia in 1991.

Table 1. Parameter values for lupin and wheat crops grown in Western Australia, 1991.

Parameter	Lupin		Wheat	
	Shoot	Root	Shoot	Root
$R_m(d^{-1})$	0.045	0.056	0.074	0.085
$C_m(gm^{-2}d^{-1})$	5.53	4.46	6.57	1.32
$t_b(d)$	74.0	69.3	50.2	44.4

can be lost so that root biomass is underestimated (Logsdon and Reneau 1988; Grzebisz et al. 1989).

Soil conditions early in the growing season are usually favorable so that there is only a small amount of root death. As the season proceeds, both natural root senescence and the incidence of unfavorable soil conditions often increase, so that it is impossible to state unequivocally the amount of dry matter that a crop has invested in its root system. Because this "turnover" of roots has not yet been reliably quantified it is difficult to be certain that the apparent differences in growth patterns between cereals and legumes discussed previously are real, or a consequence of differences in rates of root decay, determined genetically or environmentally. In the lupin and wheat crops discussed above, root weight in the upper 10 cm invariably declined at about flowering in both crops despite an overall increase in the size of the root system. For example, in 1992 the lupin root system remained constant in size between 8 Sept and 7 Oct at about 148 g m^{-2}, although root weight in the upper 10 cm decreased by 6 g m^{-2}.

The magnitude of carbon losses from roots to the soil and their impact on the soil biomass has been the subject of speculation (Martin 1977; Wood 1987). Most measurements of the fate of carbon have been made using pulse-labeling with radioactive carbon to provide estimates of carbon losses via respiration and rhizodeposition from young plants grown in controlled environments (Meharg and Killham 1990). Measurements by Martin and Kemp (1986) with wheat grown in field plots showed that a high proportion of ^{14}C translocated to the roots was released as rhizosphere CO_2 (65% at 7 weeks after emergence and decreasing to 45% at 10 weeks). Similarly, Keith et al. (1986) found at early tillering that about 50% of photosynthate was translocated below-ground, of which about one-half was respired and one-quarter was recovered from the soil and one-quarter from the roots. The pattern of partitioning and loss changed during growth so that less than 5% of the photosynthate was translocated below-ground after anthesis. Gregory and Atwell (1991) conducted a similar field experiment in Western Australia and found that in young wheat plants about 33% of the photosynthate was recovered in below-ground components, of which about one-half was from respiration (Table 2). Their results suggested only little loss to the rhizosphere by exudation. After anthesis, only 9% of photosynthate was partitioned below-ground. Over the entire season, the input of carbon to the below-ground components was 48 g C m^{-2}, of which only 3.3% was collected as exudate/sloughed material and 28% was collected as respired C.

Seasonal variations in root growth

Most studies of root systems have been in single growing seasons, so that relatively little is known about the inter-seasonal variation of root production and whether or not it reflects that of shoot growth. Welbank et al. (1974) compared the growth of spring-sown barley roots (Maris Badger) grown over a 4-year period (1966-69) and of winter wheat (Cappelle Desprez) grown over a 3-year period (1969-71). All crops were grown on a light, sandy silt loam of either Cottenham or Stackyard series and given N-fertilizer. For barley, their results showed little inter-seasonal difference in the maximum, dry weight of roots

Table 2. The distribution of ^{14}C in the soil and wheat plant system 24 hours after labeling; values in brackets are one standard error (from Gregory and Atwell 1991).

Days after sowing	% of ^{14}C recovered			
	Shoot	Root	Soil	Respiration
50	667(3.7)	17.0 (2.7)	0.4 (0.1)	15.9(2.3)
71	71.7(2.4)	22.3(2.1)	1.4(0.5)	4.7(0.6)
106	91.1 (1.0)	5.5 (0.5)	0.1 (0)	3.3 (0.5)
120	91.4 (1.6)	5.4(1.4)	0.1(0)	2.7(0.7)

produced (95 g m^{-2} in 1966 and 80 g m^{-2} in the other years), although there were differences in the rates of root growth such that the weight at 60 days after sowing ranged from 11 to 95 g m^{-2} Similarly, with winter wheat the maximum dry weight measured varied from 95 to 118 g m^{-2}, although at the end of March one crop had as little as 5-6% of its maximum weight, whereas another had 30-40%. Grain yield (85% dry matter) of these crops was similar for all seasons, ranging from 5.1 to 5.9 t ha^{-1}.

Gregory et al. (unpublished) grew barley (Beecher) at two contrasting sites in Aleppo province, northern Syria between 1981 and 1987. The first site was at Breda (35° 55'N, 37° 10'E), which lies to the south of Aleppo and has a long-term mean annual rainfall of about 280 mm, and a soil that is a pale red, clay loam (Typic Calciorthid, USDA; Calcic Xerosol, FAO). The second site was the main field station of the International Center for Agricultural Research in Dry Areas (ICARDA) at Tel Hadya (35° 55'N, 36° 55'E), which has a mean annual rainfall of about 320 mm and a soil that is a Chromoxerertic Rhodoxeralf (USDA)/Vertic Luvisol (FAO). Crops were given small amounts of N and P fertilizers and kept free of weeds. Samples were taken at several times, but one was taken as close to flowering as practical (usually in mid-April) and was used as the basis for comparisons.

Root weight for crops at Breda that were given fertilizer varied between seasons from 35.2 to 106.8 g m^{-2} for Beecher (Table 3). The smallest root weight was recorded in 1983/84, although this was not the driest season. However, rainfall during early growth in Dec, Jan, and Feb 1983/84 (73 mm) was less than that in 1985/86 (113 mm) and clearly had a marked effect on growth. Root length varied similarly to root weight, although the correspondence was not exact. It is noteworthy that the seasons of above-average rainfall (1981/82 at Breda and 1984/85 at Tel Hadya) resulted in long root systems. With the exception of 1984/85, root systems at Tel Hadya were smaller than those at Breda. Overall, length and weight were closely related, giving a specific root length for all crops at both sites of 0.193 km g^{-1} (Fig. 4).

At anthesis, root weight as a proportion of total plant weight ranged from 0.25 to 0.13 at Breda with the highest proportions generally occurring in the two driest seasons (1983/84 and 1985/86). However, the proliferation of roots in the wetter-than-average season of 1982 resulted in the second highest proportion (0.19). At Tel Hadya, the combination of heavier shoots and lighter root systems gave root:total plant proportions of 0.06 in both 1985/86 and 1986/87. As with the wetter than average season at Breda, the 1984/85 season gave the greatest proportion of dry weight as roots of about 0.13.

Table 3. Seasonal production of roots and shoots and the partitioning of dry matter for crops of barley (Beecher) grown in northern Syria.

Site	Season	Root dry weight (g m^{-2})	Root length (km m^{-2})	Shoot dry weight (g m^{-2})	Root total weight
Breda	81/82	106.8	16.2	462	0.19
	82/83	58.5	73	342	0.15
	83/84	35.2	2.7	159	0.18
	84/85	57.4	95	393	0.13
	85/86	50.8	9.2	149	0.25
	86/87	61.4	9.1	399	0.13
Tel Hadya	84/85	108.1	21.9	775	0.12
	85/86	36.8	6.7	610	0.06
	86/87	46.9	6.9	732	0.06

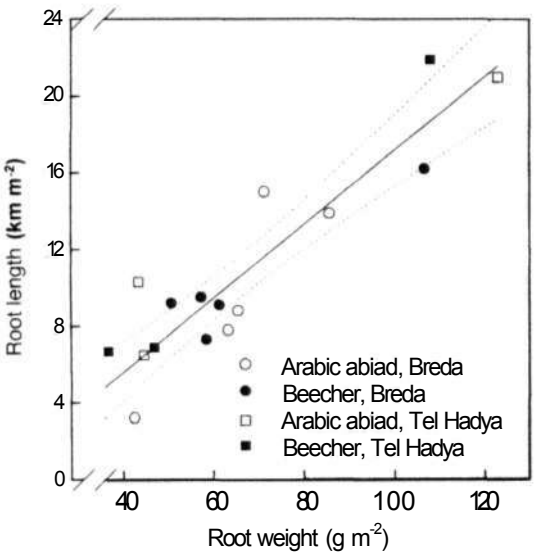


Fig. 4. Relation between root length and dry weight at anthesis for two genotypes of barley (Arabic abiad and Beecher) grown in northern Syria at Breda, and at Tel Hadya. The straight line is the linear regression with other lines showing 95% confidence interval (y - 0.193x - 2.124; r^2 = 0.92).

Rooting depth and distribution

The potential depth of rooting is determined genetically. For example, Hamblin and Hamblin (1985) grew lupin (*Lupinus* spp.), pea (*Pisum sativum* L.), and wheat on three deep sands (xeric psamments) with rainfall ranging from 155 to 428 mm in Western Australia and found that the maximum rooting depth was significantly different ($p < 0.001$) between genotypes and species, but not between sites. Rooting depth averaged 190 cm for lupin, 65 cm for pea, and 113 cm for wheat. However, in practice, soil conditions also play an important role in determining rooting depth, so that, for example, lupin *(Lupinus angustifblius)* and wheat planted on a duplex soil in Western Australia both rooted to 80 cm because of physical impediments to growth in both the sand and clay layers and because of

the restricted depth of soil re-wetting by rain (Dracup et al. 1993; Gregory and Eastham 1996).

Borg and Grimes (1986) reviewed the depth of rooting of 48 crop species and found that the time course of rooting could be described by an empirical sine function. To use the function, the length of the growing season and the maximum depth of rooting need to be known. While the former is usually known with some certainty, it is the variability of the latter depending on soil conditions that limits the predictive value of such equations. For much of the growing season, rooting depth increases linearly with time (Monteith 1986; Robertson et al. 1993b). Gregory and Eastham (1996) measured the rate of downward root penetration of lupin and wheat crops for three consecutive seasons and found rates of 5.2 mm d^{-1} for lupin and 8.7 mm d^{-1} for wheat (Fig. 5). Lupin crops continued to grow downwards for about 30-40 days after flowering started, but wheat roots reached their maximum some 30 days before flowering.

The distribution of roots of field crops within the soil profile has been described by simple, empirical equations by Gerwitz and Page (1974) and by Greenwood et al. (1982). Greenwood et al. (1982) assumed that, for a crop growing on a uniform soil profile, the gradient of root length density with depth at any given time is proportional to the root length density (L_v) at that depth (z), i.e.,

$$dL_v/dz = -qL_v \qquad (2)$$

where q is constant with depth but varies with time. Integration with respect to z gives

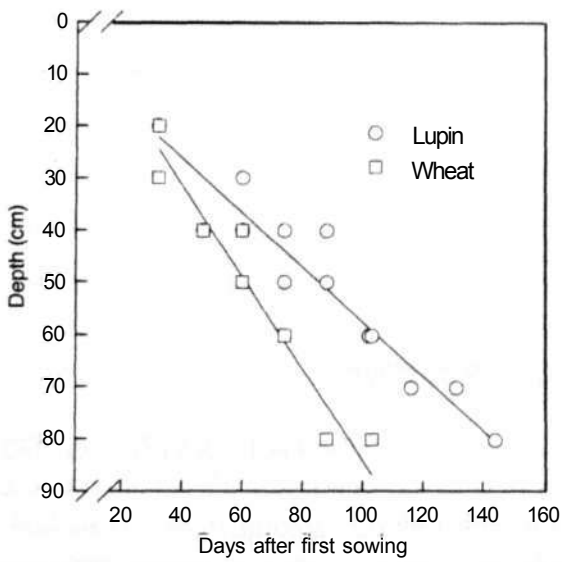


Fig. 5. Depth of rooting for crops of lupin and wheat grown on a duplex soil at East Beverley, Western Australia (from Gregory and Eastham 1996),

$$L_v = L_{v0}\ exp^{-qz} \quad (3)$$

where L_{vv} is the root length density at depth 2 = 0. This means that a graph of ln L_v against z should give a straight line with intercept L_{vo} and gradient $-q$. Figure 6 shows seasonal changes in root length density for a crop of barley grown in northern Syria. Equation 3 describes the profiles well, particularly during early growth, and reasonably well later in the season except towards the base of the rooting profile where root lengths were small. This divergence towards the base of the profile occurs because not only are the root lengths small and subject to large errors in sampling, but also the roots at this depth consist of a few unbranched axes so that root length density does not change with depth. It is clear from Figure 6 and other studies that not only do the rooting depth and quantity of roots increase with time but that the slope of the line (q) decreases with time. Greenwood et al. (1982) showed that q was related to the depth containing 90% of the root length (z_{90}) by

$$z_{90} = (\ln\ 10)/q \quad (4)$$

so that as q becomes smaller during the season as z_{90} increases.

Although these equations may provide a useful description of root distribution, their predictive value is limited because we cannot quantify the environmental factors determining q. Gregory (1994) has discussed these limitations and shown the seasonal variation that occurs in q with crops of wheat. Brown et al. (1989) showed a similar seasonal and site dependence of q for crops of chickpea.

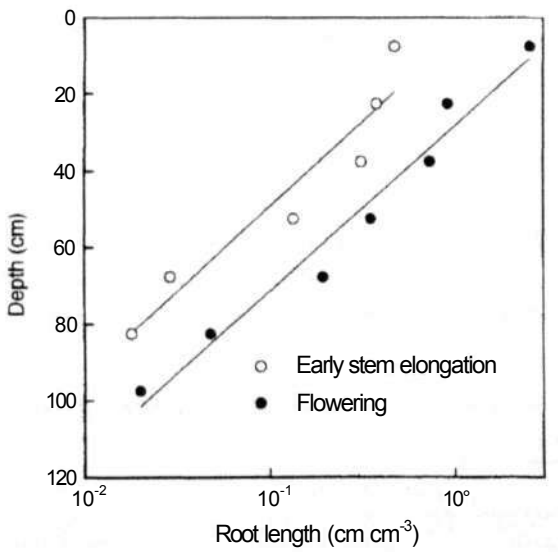


Fig. 6. Change in root length with soil depth between early stem elongation and flowering for Beecher barley grown at Breda, northern Syria (data from Brown et al. 1987).

Where soils are uniform with depth, equation 3 has provided an adequate description of root distribution. However, there are many circumstances where root distribution is not of this form, and both impediments to, and stimulation of, growth may occur in specific soil layers. For example, Gregory and Squire (1979) found the maximum L_v of pearl millet crops grown on an Alfisol at the International Crops Research Institute for the Semi-Arid Tropics (ICR1SAT), Hyderabad, India to be at 30 to 40 cm depth; this was immediately above a compact murrum layer, which is a zone of clay and N accumulation. A similar accumulation of roots above a zone of soil that usually appeared impeded was reported for pea grown on a sandy loam at Sutton Bonington, U.K. (Dawkins et al. 1984). Accumulation of nutrients has long been known to stimulate root growth, and in column experiments in which nitrate was leached, L_v at 95 cm was as great as that in the upper 10 cm of soil (Diggle et al. 1990). In this latter experiment, Diggle et al. (1990) found that by the addition of a bell-shaped component to equation 3, they could adequately describe the root profiles observed.

Water uptake by root systems

Monteith (1986) suggested an analytical framework for examining the pattern of water extraction by an expanding root system from a continuously drying soil profile. It is essentially comprised of two functions, the first describing the downward movement of the extraction front or rooting depth (shown to be the same in specified circumstances) and the second describing the extraction by a static root system. In a continuously drying system, extraction begins in a layer as soon as the rooting front reaches it, but in the winter rainfall environment of mediteranean climates, the development of an observable drying front may be several weeks behind that of the actual rooting depth (Table 4).

When extraction begins in a layer, the volumetric water content (6) decreases with time following a relation described by Passioura (1983):

$$\theta = \theta^* \exp[-kL_v(t-t_c)] \quad (5)$$

where θ^* is the maximum amount of water that roots are capable of extracting from the soil layer, k is a time constant, and $t - t_c$ is the duration of the exponential decay that starts in a layer at time t_c. The quantity $1/kL_v$ can be regarded as a time constant and roots move

Table 4. Comparison of the depth of the rooting front and the depth of the water extraction front for crops of lupin and wheat, 1990.

Days after	Lupin		Wheat	
sowing	Root depth (cm)	Extraction depth depth (cm)	Root depth (cm)	Extraction depth (cm)
32	20		30	30
60	40	30	50	45
88	60	45	80	50
116	80	60	>80	60
144	80	70		

downward to arrive at depth z at time t_z. Robertson et al. (1993a) found that although the rate of downward progress of the extraction front was a conservative quantity for six different crops of sorghum, the value of $1/kL_v$ varied considerably depending on variations in L_v and evaporative demand.

Monteith (1986) and Robertson et al. (1993b) were unable to use equation 5 to describe changes of water content in the upper 30 cm and 50 cm of soil, respectively, presumably because of substantial evaporation directly from the soil surface. However, in Western Australia where crops have reached an appreciable size before depletion of the soil water reserve occurs, equation 5 described the depletion of soil water from layers to within 10 cm of the soil surface (Fig. 7). Table 5 shows that $1/kL_v$ did not change consistently with depth, but was larger in the clay horizon (40 and 50 cm) than the sand layer. It is noteworthy that the depletion from each layer was of the form described by equation 5, despite the fact that L_v was not constant during the period of depletion. Robertson et al. (1993a) noted that L_v will change during the extraction period so that k represents an "average" diffusivity for the duration of extraction. Presumably in the present results, any increase of L_v was compensated for by a decrease in k because as the soil dried, soil water diffusivity did not remain constant as initially assumed by Passioura (1983). It seems odd, however, that the compensation should be so exact, particularly given the almost five-fold larger length of the wheat root system compared with that of the lupin root system. Several researchers (Hamblin and Tennant 1987; Gregory and Brown 1989) have commented upon the ability of legume root systems to extract water at the same rate as cereals despite the smaller root length. This is difficult to resolve in relation to equation 5 unless there are substantial differences in the gradients of water potential generated by the two crop types. Hamblin and Tennant (1987) demonstrated that the bulk soil water potential of wheat and lupins was similar (as was also the case in the 1990 crops) and hypothesized that the difference between crops was due to the difference in axial resistance of the root. They estimated that the axial resistance of wheat roots was some 1000 times greater than that of lupin roots.

One problem with models of water uptake based on equation 5 is that when a soil profile has been wetted, uptake should be related to the root length and gradient of hydraulic head in each layer so that water uptake will occur in each layer. This is not usually observed in practice and it is common for water uptake to occur preferentially from surface layers with uptake from depth occurring only after substantial quantities of water have been removed from the upper layers. The results obtained with the wheat and lupin crops are of this form. Gardner (1983 and 1991) has developed the hypothesis that water uptake can be described by a distributed sink moving downward. He argued that the root system tends to linearize the otherwise highly non-linear soil/water flow system so that the upper portion of the root system is characterized by a soil/plant water diffusivity that is independent of soil water content. In the lower portion of the root system there is a transitional zone before non-linear flow again applies. Such a model gives good agreement with field-derived data and describes well the situation when the surface is re-wetted because the sink moves back to the surface and moves downward at a rate dependent on the water content of each soil layer.

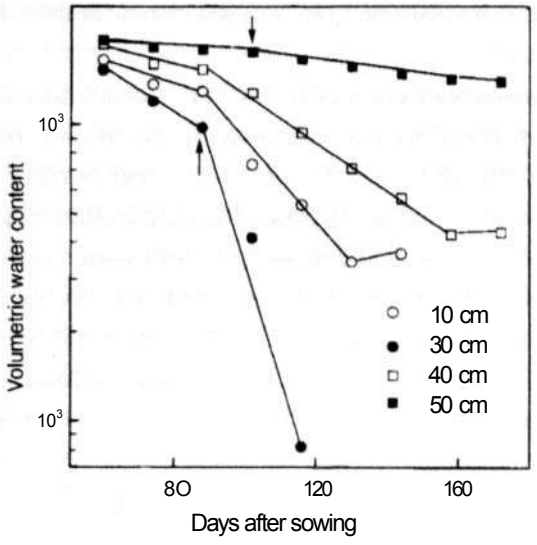


Fig. 7. Change in volumetric water content of soil beneath wheat at East Beverley, Western Australia in 1990. The arrows indicate the start of water extraction from the layer.

Table 5. Results of regressions of $\log_e\theta$ with time (days after sowing) for crops of wheat and lupin, 1990.

Crop	Depth (cm)	Time interval (days after sowing)	r^2	I/kL_v (days)
Wheat	10	88-130	0.99	32.6
	20	88-116	0.85	22.2
	30	88-116	0.97	11.3
	40	88-158	1.00	53.7
	50	102-158	1.00	273
Lupin	10	88-130	0.98	43.1
	20	88-130	0.88	17.0
	30	88-144	0.95	24.5
	40	88-158	0.98	97.7
	50	88-158	0.99	275

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Growth, Carbon Allocation, and Respiration as Affected by Nitrogen Supply: Aspects of the Carbon Balance

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Abstract

This paper describes the respiratory characteristics of roots. Firstly, a small review is given on the carbon utilization in root respiration, expressed as fraction of that imported into the roots and expressed as a fraction of that fixed in photosynthesis. Secondly, the respiratory energy requirements for the maintenance of biomass, root growth, and ion uptake were incorporated into a vegetative growth model Using this model, the biomass production of inherently fast-growing and slow-growing species was simulated under various conditions. Seedlings were pre-grown either at a high or an intermediate nitrogen supply. Thereafter they were transferred to a low constant nitrogen supply or a fluctuating low nitrogen supply. The outcome of these simulations suggest that biomass production is highly dependent on the nitrogen availability of the seedlings before they were transferred to low nitrogen supply and on the type of nitrogen supply. Under conditions of a low constant nitrogen availability, the fast-growing species produced at least an equal amount or more biomass than the slow-growing species. In the case of a fluctuating nitrogen availability, the slow-growing species produced more biomass. These results are discussed in terms of carbon gain in photosynthesis and carbon utilization in respiration.

In the case of a fluctuating nitrogen supply, the relative contribution of the carbon utilization for the maintenance of biomass, root growth, and ion uptake to the total carbon utilization in root respiration continuously shift. This suggest that each of these processes have to be taken into account, when modeling plant growth under the condition where the nitrogen availability fluctuates.

Introduction

Plants require both nutrients and carbon for their growth. Based on economic principles, Bloom et al. (1985) suggested that a high level of carbon and nutrient gain can only be

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attained if the recently fixed resources are optimally partitioned between the maintenance of the already existing biomass and the construction of new biomass. Prerequisite for this maximization principle is that newly fixed resources by themselves again are optimally partitioned between organs that are involved in the capture of resources. Already in the 1960s, Brouwer (1963) suggested that in response to a shift in resource supply, plants invest most of their resources in the organ that is involved in the capture of the limiting resource. For instance, under conditions of low light, most of the fixed carbon and nutrients are spent on shoot growth, whereas under conditions of nutrient limitation they are spent on root growth. Based on simulation studies, Van der Werf et al. (1993a) suggested that allocation of recently fixed carbon and nitrogen to shoots and roots are optimized, resulting in a maximization of relative growth rate, irrespective of species and nitrogen supply. Optimization of resource allocation to shoots and roots automatically implies that the carbon gain in photosynthesis and carbon utilization in respiration are in dynamic state upon change in the nitrogen supply. Thus, optimization strongly influences the carbon balance of a plant. For example, with decreasing nitrogen supply, the amount of carbon utilized in root respiration expressed as a fraction of that fixed in photosynthesis increases dramatically (Van der Werf et al. 1992a, 1994).

In this paper I firstly analyze effects of a reduced nitrogen supply on (a) shoot /root ratio and allocation of recently fixed carbon and nitrogen to shoots and roots, (b) carbon utilization in root respiration, and (c) respiratory energy costs for maintenance of biomass, growth, and ion uptake. These plant characteristics are discussed for inherently fast- and slow-growing wild plant species, which generally are predominant in nutrient-rich and nutrient-poor environments, respectively. Secondly, using a simulation model, comparisons are made between the carbon budget of a fast- and a slow-growing plant species grown at a constant low nitrogen availability and grown at a similar but fluctuating nitrogen availability. The simulation results show that the type of nutrient availability (constant or fluctuating) strongly influences biomass production and the carbon balance.

Shoot/root ratio

When species from nutrient-poor and nutrient-rich habitats are compared under conditions of optimal nitrogen supply, generally only marginal differences in shoot/root ratio are observed (Poorter and Remkes 1990, Hunt et al. 1987, Van der Werf 1996). It is now generally believed that when species are grown under conditions of optimal nitrogen supply, differences in relative growth rate between species are mainly explained by differences in specific leaf area (leaf area per unit leaf weight) and are only partly explained by differences in the investment of biomass in shoots versus roots (Poorter and Remkes 1990, Lambers and Poorter 1992, Van der Werf et al. 1993b). However, simulation studies show that differences in shoot/root ratio at a given nitrogen supply strongly influence the relative growth rate of a species (Van der Werf et al. 1993a).

The shoot/root ratio drastically decreases with a reduction in nitrogen supply (Klepper 1991). Surprisingly, under these conditions of low nitrogen supply, fast-growing species that are adapted to a nutrient-rich environment, generally invest more of their

biomass in roots than slow-growing species that are adapted to nutrient-poor conditions (e.g., Christie and Moorby 1975). This may be one of the reasons why fast-growing species always produce more biomass than slow-growing species, even under conditions of low nutrient supply, at least in short term experiments (Van der Werf et al. 1993b).

Although changes in shoot/root ratio are generally explained by the "functional equilibrium" principle (Brouwer 1963, 1983), its physiological regulation remains obscure (Van der Werf 1996). At present several different hypotheses on the regulating mechanisms of shoot-root interactions can be seen in the literature. Jackson (1993) reviewed an extensive amount of papers, most of which suggested that hormones in some way would be involved in the regulation of the shoot/root ratio. On the contrary, Farrar (1992) explained the regulation of the shoot/root ratio without any involvement of hormones. In his model, sucrose is placed as the main messenger between source and sink and vice versa. Both short term effects of sucrose on allocation and its long term effects on gene expression are included in the model. Van der Werf (1996) and Van der Werf and Nagel (1996), integrated the hormone and sucrose explanations into one hypothesis. In this model, nitrogen supply affects the rate of cytokinin production in root tips and regulates the turgor pressure gradient between sources and sinks through a change in sucrose concentration. In the long run, cytokinins and sucrose have an antagonistic effect on some key enzymes. Until now none of these hypotheses have been analyzed sufficiently, thus no explanation can be given for the optimization patterns seen in plants.

The shoot/root ratio is the consequence of carbon and nutrient allocation to shoots and roots and the carbon losses in shoot and root respiration. Under conditions of near-optimal nitrogen supply, the allocation of carbon and nitrogen is directed towards the shoot, whereas under conditions of extremely low nitrogen supply, it is towards the root (Van der Werf et al. 1993c).

Carbon utilization in root respiration

Depending on species and growth conditions, between 30 and 75% of all carbohydrates imported into the roots are utilized in respiration (Lambers et al. 1991). At a high supply of

Table 1. Relative growth rate (RGR, mg g^{-1} day^{-1}) and carbon utilization (C-utilization) in root respiration expressed as a percentage of that imported into the root for inherently fast- and slow-growing species grown at high nitrogen supply (HN) and low nitrogen supply (LN). Data derived from the relative growth rates of the roots and the rate of root respiration, assuming a carbon content of 40% and a respiratory quotient of 1.2 (from Van der Werf et al. 1993d). Cf *Carex flacca;* Bm *Briza media;* Bp *Brachypodium pinnatum;* Dg *Dactylis glomerata;* Hl *Holcus lanatus*

Species	HN		LN	
	RGR	C-utilization	RGR	C-utilization
Cf	104	46	39	58
Bm	113	49	44	60
Bp	150	47	36	62
Dg	213	41	35	58
Hl	238	36	39	58

nitrogen both fast- and slow-growing species respire approximately 40% of the imported carbon. This fraction increases to approximately 60% at extremely low nitrogen supply (Table 1). The increase in respiratory utilization of carbon with decreasing nitrogen supply can be explained by a constant requirement of energy for maintenance processes, and an increase in the specific respiratory energy costs for maintenance and/or ion uptake as will be discussed below (Van der Werf et al. 1994).

A significant portion of the daily fixed carbon in photosynthesis is respired again in roots. Under conditions of high nitrogen supply average carbon utilization in root respiration are approximately 9% of the daily carbon gain for fast-growing species and about 18% for a slow-growing species (Poorter et al. 1990). This fraction increases dramatically (up to 50%) when the nitrogen supply is reduced (Van der Werf et al. 1992a). This increase is due to a sharp decrease in carbon-gain in photosynthesis and a large increase in root biomass relative to plant biomass. Since the roots are a major sink for carbohydrates, more attention should be paid to the processes determining root respiration.

Respiratory energy costs for the maintenance of biomass, growth, and ion uptake

Respiration is the driving force for the maintenance of biomass, growth, and ion uptake (Veen 1980, Van der Werf et al. 1988). Maintenance of biomass depends on two important processes: (1) turnover of proteins (Penning de Vries 1975, De Visser et al. 1992, Van der Werf et al. 1992b) and (2) maintenance of electrochemical gradients across membranes (Bouma and De Visser 1993). The specific cost for the synthesis of biomass largely depends on the biochemical composition of the newly synthesized biomass (Penning de Vries et al. 1974, Poorter 1992). Anions are taken up against an electrochemical gradient and therefore require substantial amounts of respiratory energy (Clarkson 1985, McClure et al. 1990a, b, Wieneke 1992).

Under conditions of high nitrogen supply, 10-15% of the total rate of root respiration is ascribed to the maintenance of biomass. Fast-growing species spend around 50% of their total energy produced by root respiration for ion uptake, whereas slow-growing species spend up to 70%. Biosynthesis consumes 20 and 30% of the total energy production in root respiration of slow- and fast-growing species, respectively (Poorter et al. 1991). With decreasing nitrogen supply, both the relative growth rate and the rate of ion uptake decrease and most of the energy production in root respiration is spent for the maintenance of root biomass (Van der Werf et al. 1992a).

The respiratory energy (ATP) in plants is provided by two different pathways: the cytochrome pathway, yielding three ATP per oxygen reduced, and the less efficient alternative pathway, yielding only 1 ATP per oxygen reduced. The regulation of partitioning of electrons via the two pathways is presently under debate (Atkin et al. 1995). The classical view is that the alternative pathway can only become engaged when the cytochrome pathway is fully saturated. Atkin et al. (1995) pointed out the invalidity of this hypothesis based on an evidence that the alternative pathway was engaged before full saturation of the cytochrome pathway. In addition, recent developments regarding the

regulation of electron flow via the alternative and cytochrome pathways suggest that the use of specific inhibitors of the two pathways may not necessarily give a good indication of the activities of both pathways (Millar et al. 1995). Stable isotope (^{18}O) techniques look promising for non-invasive measurement of the electron flow via the alternative and cytochrome pathways.

A large variation in the rate of root respiration exists among species. We now can attribute these differences to the activity of the alternative pathway, the specific respiratory energy costs for the maintenance of biomass, growth and ion uptake, and in the rates of each of these processes.

When grown at a high nitrogen supply, fast-growing species, generally have a higher rate of root respiration than slow-growing species (Poorter et al. 1991, Van der Werf et al. 1993d). These differences can not be explained by differences in the activity of the alternative pathway (Poorter et al. 1991; note that these results were obtained using specific inhibitors for the alternative and cytochrome pathways and that these may not necessarily give a realistic picture of the activity of the alternative pathway in vivo). The higher rate of root respiration of the fast-growing species compared with that of the slow-growing species can be explained by the higher relative growth rate of the roots and the higher rate of ion uptake per unit root weight (Poorter et al. 1991, Van der Werf et al 1992a). However, the difference in root respiration between the fast- and slow-growing species was not as high as expected from the difference in growth and ion uptake between the two types of species. Fast-growing species have slightly higher costs for biosynthesis than slow-growing species. The relatively small difference in the rate of root respiration between inherently fast- and slow-growing species (despite their large difference in growth and ion uptake) can be explained by the far lower respiratory energy costs for ion uptake in the fast-growing species.

At low nitrogen supply, the interpretation of the measured rates of root respiration becomes more difficult. The specific rate of root respiration decreases both in fast- and slow-growing species, but not as much as that expected from the reduction in rates of growth and ion uptake (Van der Werf et al. 1992a). With decreasing nitrogen supply, the specific costs for maintenance and/or ion uptake should increase. Van der Werf et al. (1994) give possible explanations for this increase.

Next the specific respiratory energy requirements for maintenance of biomass, growth, and ion uptake are integrated in a vegetative growth model. With the aid of this model the carbon balance of a fast-and a slow-growing species will be analyzed under conditions of stable and fluctuating nitrogen availability of the soil.

In general, fast-growing species produce more biomass in the short run than slow-growing species, irrespective of the nitrogen supply (e.g., Berendse et al. 1992). This actually is quite peculiar as slow-growing species are dominant in nutrient-poor habitats, whereas fast-growing species are generally absent. The following simulation study shows that the outcome of such experiments may be partly due to the conditions under which the seedlings were grown before the experiment started. In addition, the results show that both conditions of nitrogen supply (constant or fluctuating) lead to differences in biomass production. In the following discussion, special emphasis is given to the carbon utilization in root respiration.

Modeling growth and the carbon balance

The vegetative growth model consists of a set of differential equations for the growth of leaves (1), "stems" (2), and roots (3; see Van der Werf et al. 1993a, c for more information):

$$dW_1/dt = (\alpha_{cl}\varphi W, - \rho_l \quad W_1)/C_{cl} \quad (1)$$

$$dW_s/dt = (\alpha_{cs}\varphi W_1 - \rho_s \quad Ws)/C_{cs} \quad (2)$$

$$dW_r/dt = [(\alpha_{cr}\varphi W_1 \quad - r_m W_r - C_{nu} dN_p/dt)/(1 + \quad C_g/C_{cr})]/C_{cr} \quad (3)$$

where dW_1/dt, dW_s/dt, and dW_r/dt are the absolute growth rates of leaves, stems and roots, respectively, α_{cl}, α_{cs} and α_{cr} are the allocations of carbon to leaves, stems, and roots, respectively, expressed as a fraction of recently fixed carbon in photosynthesis, φ is the rate of photosynthesis per unit leaf weight and is dependent on the leaf nitrogen concentration, ρ_l and ρ_s are the rates of respiration per unit of leaf and stem weight, respectively, r_m is the amount of carbon utilized in root respiration for maintenance processes, c_g and c_{nu} are the amounts of carbon utilized per unit of biomass produced and per unit of nitrogen taken up, respectively, C_{cl}, C_{cs} and C_{cr} are the carbon contents of leaves, stems and roots, respectively. The rate of nitrogen uptake (dN_p/dt) is described by:

$$dNp/dt = \quad \sigma W_r \quad (4)$$

where σ is the rate of nitrogen uptake per unit root weight. The nitrogen availability of the soil is modeled via its effect on σ. The allocation of recently fixed carbon and nitrogen to shoots and roots are described as a function of the internal plant nitrogen concentration (Van der Werf et al. 1993c, Van der Werf and Nagel 1996). Any change in nitrogen availability will lead to changes in plant nitrogen concentration and thus to changed allocations of carbon and nitrogen to shoots and roots, changed leaf nitrogen concentrations and thus to changed rates of photosynthesis. The model simulates plant parameters quite well, both under steady-state conditions and non-steady-state conditions (Van der Werf et al. 1993a, c, Van der Werf and Nagel 1996)

Next, the model is applied to plants of a fast-growing (*Dactylis glomerata* L) and slow-growing (*Briza media* L) monocotyledonous species that were firstly grown at a nitrogen availability, allowing a near-maximum growth rate or they were firstly grown at an intermediate nitrogen supply (Fig. 1). Under the conditions of a high and constant nitrogen availability, the nitrogen availability for the fast-growing species was such that it matched an uptake rate of nitrogen of almost 2 mmol N g^{-1}(root) day^{-1}, whereas that for the slow-growing species was approximately 1 mmol N g^{-1} (root) day^{-1}. Under the conditions of an intermediate nitrogen supply for seedling growth, the nitrogen availability was such that it matched an uptake rate of 0.7 mmol g^{-1} (root) day^{-1} for both species. When the seedlings were pre-grown at a high nitrogen supply, the fast-growing species achieved a relative growth rate of 213 mg g^{-1} day^{-1}, and the slow-growing species a relative growth rate of 113 mg g^{-1} day^{-1}. In the case of an intermediate nitrogen availability, relative growth rates of

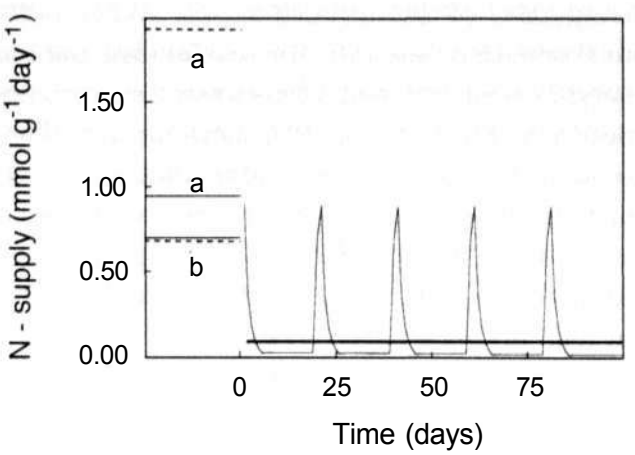

Fig. 1. Simulated experimental set-up. Seedlings of a fast-growing species (dotted line) and a slow-growing species (solid line) were (a) pre-grown first at a nitrogen availability (expressed in terms of the uptake rate per unit root weight) to sustain a maximum relative growth rate (a), or (b) were first pre-grown at an intermediate nitrogen availability. When the seedlings reached a weight of 0.01 g, they were transferred to either a constant low nitrogen availability (thick line) or a fluctuating availability (thin line). Integrated with time, both treatments had the same nitrogen availability.

approximately 160 and 110 mg g^{-1} day^{-1} were achieved for the fast- and slow-growing seedlings, respectively. Next, the seedlings were transferred to constant and a low nitrogen availability, sustaining a constant uptake rate of 0.1 mmol N g^{-1}(root) day^{-1}, or to a similar but fluctuating nitrogen availability. In the case of the fluctuating nitrogen availability, the total availability with time is the same as for the constant nitrogen availability.

Simulation results

One hundred days after a transfer from a high to a constant lOW nitrogen supply, the fast-growing species produced approximately 19% more biomass than the slow-growing species (Table 2). This difference is due mainly to the higher relative growth rate of the fast-growing species immediately after the transfer (data not shown). These simulation results agree with experimental results (e.g. Bradshaw et al. 1964, Hull and Mooney 1990, Poorter 1991, Berendse et al. 1992): fast-growing species always produce more biomass than the

Table 2. Total simulated amount of biomass (g DW) after 100 days for a fast- (*Dactylis glomerata* L.) and slow-growing (*Briza media* L.) species. Treatments were (see also Fig. 1): (a) HNC, seedlings pregrown at a high nitrogen supply and thereafter transferred to a constant nitrogen availability, sustaining an uptake rate of 0.1 mmol g^{-1} (root) day^{-1}; (b) HNF seedlings pregrown at a high nitrogen supply and thereafter transferred to a similar nitrogen availability as HNC, but fluctuating; (c) INC seedlings pregrown at an intermediate nitrogen supply and then transferred to a nitrogen availability, sustaining an uptake rate of 0.1 mmol g^{-1}(root) day^{-1} ; (d) INF seedlings pregrown at an intermediate nitrogen supply and then transferred to a similar nitrogen availability as INC, but fluctuating.

Species	HNC	HNF	INC	INF
Fast	6.01	3.43	4.28	2.58
Slow	5.06	3.70	435	3.19

slow-growing species, irrespective of the nitrogen supply. When both types of species experienced a similar, but fluctuating, low nitrogen availability, the biomass production was severely reduced (43 and 27% for fast- and slow-growing species, respectively). In this case the slow-growing species produced approx. 8% more biomass than the fast-growing one. These shifts in species advantage become even more striking, when the seedlings were firstly grown at an intermediate nitrogen supply. When seedlings were transferred from an intermediate nitrogen supply to a low constant nitrogen supply, both the fast- and the slow-growing species produced less biomass (29 and 14%, respectively) compared with seedlings pre-grown at an high nitrogen supply (Table 2). In this case, both the fast- and slow-growing species produced equal amounts of biomass. When seedlings were pre-grown first at an intermediate nitrogen supply and then transferred to a low but fluctuating nitrogen supply, the biomass production decreased even further (57 and 37% for the fast- and slow-growing species, respectively) compared with seedlings grown at a high nitrogen supply and transferred to a constant low nitrogen supply. Surprisingly, when seedlings were firstly grown at an intermediate nitrogen supply and thereafter transferred to a low fluctuating nitrogen availability, the slow-growing species produced 24% more biomass than the fast-growing species.

Next, a case study on the effects of nitrogen supply on the carbon balance is examined. The responses of the fast- and slow-growing species will be analyzed for seedlings which were firstly grown at an intermediate nitrogen supply and subsequently transferred to a low constant or fluctuating nitrogen supply.

Under a low constant nitrogen supply, the relative growth rate of both species is similar (Fig. 2). In the case of a fluctuating nitrogen supply, the relative growth rate of the fast-growing and slow-growing species increases upon a sudden flush of nitrogen. Several days after this flush, the fast-growing species have a higher relative growth rate. However, most of time the slow-growing species are able to maintain a higher relative growth. Consequently, slow-growing species produce more biomass (24%) than fast-growing ones (Table 2). This can be explained by a close examination of Figure. 3. The fast-growing species maintain an equal or higher carbon gain in photosynthesis per unit plant weight than the slow-growing species. The total respiratory carbon utilization, expressed as a percentage of those fixed in photosynthesis, in shoots and roots is higher in the fast-growing species. Consequently, several days after the flush, the relative growth rate of fast-growing species is lower than that of the slow-growing species. The higher utilization of carbon in root respiration (expressed as percentage of those fixed in photosynthesis) for the fast-growing species are mainly explained by their lower shoot/root ratio (Fig. 1). The simulated respiratory utilization of carbon in root respiration is lower than that measured in experiments (see Van der Werf et al. 1992a, 1994). This is mainly due to the assumption that the respiratory energy costs for maintenance, growth, and ion uptake obtained under conditions of a high nitrogen supply, can be applied to conditions of low nitrogen supply. However, there is recent evidence that the specific costs for maintenance and/or ion uptake are higher at low nitrogen supply than at high nitrogen supply (Van der Werf et al. 1994). Figure 4 shows the carbon utilization in respiration for the maintenance of biomass, root growth, and ion uptake relative to carbon gain in photosynthesis. Most of the carbon is spent for maintenance, except in the case of a sudden flush of nitrogen, when uptake

contributes significantly to the total carbon utilization in root respiration. Under conditions of a low nitrogen supply, the maintenance of biomass is the most important process in root respiration (expressed per unit root weight), whereas ion uptake only consumes a small part of the total respiratory energy (Fig. 4). At optimal nitrogen supply, however, growth, and ion uptake consume most of the respiratory energy (Poorter et al. 1991).

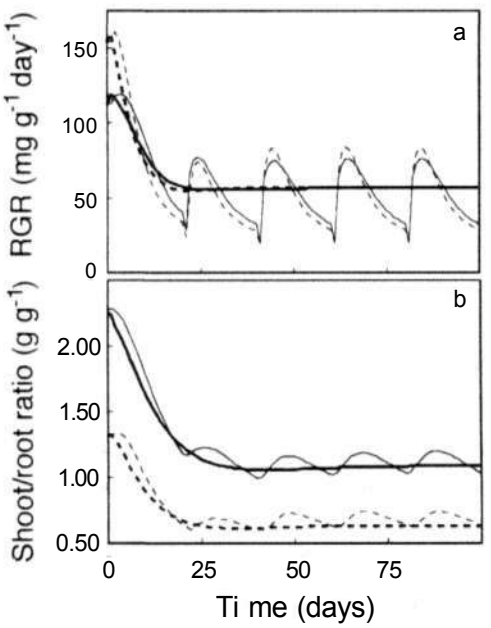

Fig. 2. Simulated relative growth rate (RGR, a) and shoot/root ratio (b) of a fast-growing species (dotted lines) and slow-growing (solid lines) species at either constant (thick lines) or fluctuating (thin lines) nitrogen availability. Before the transfer to a low nitrogen availability seedlings were pre-grown first at an intermediate nitrogen availability. (see legend Fig. 1.)

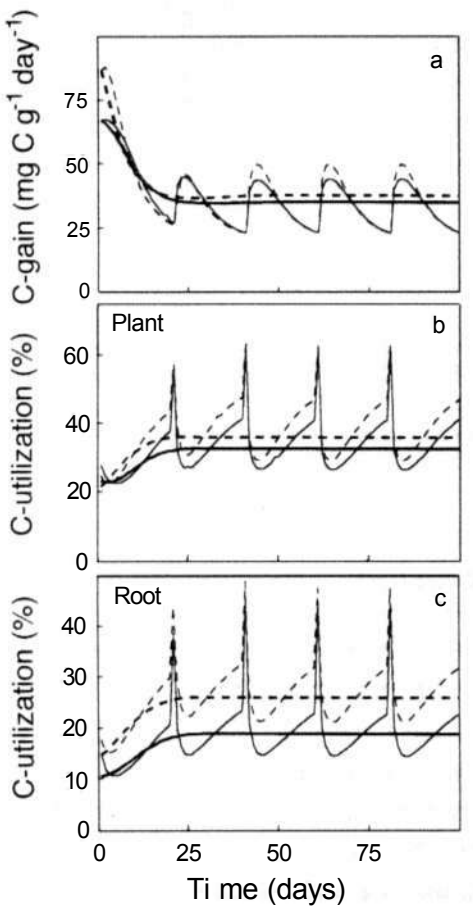

Fig. 3. Simulated rate of carbon gain in photosynthesis per unit plant weight (a), simulated carbon utilization in shoot plus root respiration, expressed as a percentage of that fixed in photosynthesis (b) and simulated carbon utilization in root respiration, expressed as a percentage of that fixed in photosynthesis (c) of a fast-growing species (dotted lines) and slow-growing (solid lines) species at either constant (thick lines) or fluctuating (thin lines) nitrogen availability. Before the transfer to a low nitrogen availability seedlings were pre-grown first at an intermediate nitrogen availability. (see legend Fig. 1.)

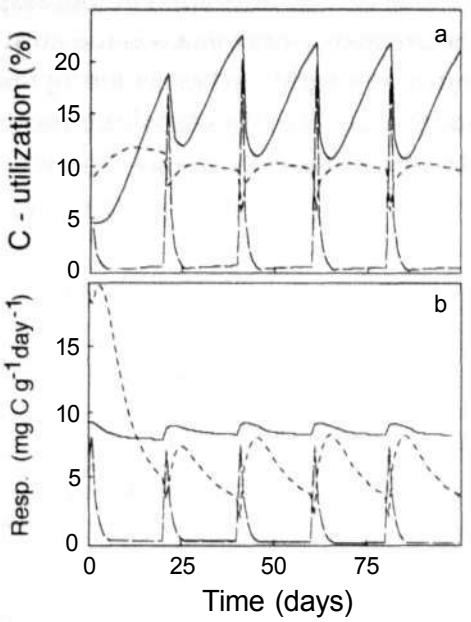

Fig. 4. Simulated carbon utilization (expressed as a percentage of that fixed in photosynthesis) in the maintenance of root biomass (————), root growth (. . . . .) and ion uptake (————) of a fast-growing species (a) and simulated rates of maintenance, growth, and ion uptake respiration in roots (b). Seedlings were pre-grown first at an intermediate nitrogen availability and then transferred to a low fluctuating nitrogen availability, (see legend Fig. 1).

Conclusion

The outcome of these simulation results suggest that biomass production within a species is highly dependent on the type of nitrogen availability. Within a treatment, differences in production may well differ up to 50%. These results suggest that under conditions of a high heterogeneity of the nitrogen availability of the soil, heterogeneity can not be ignored, when modeling crop growth under field conditions.

Another outcome from this simulation involves the interpretations of experiments in which fast- and slow-growing were compared under nutrient-poor conditions. The general conclusion of these experiments is that slow-growing species, even though they are characteristic for nutrient-poor habitats, are not better adapted to low nutrient availabilities in terms of carbon and nutrient gain: slow-growing species generally produce less biomass than fast-growing species, even at a low nitrogen supply. This simulation study confirms these experimental results, at least when species where grown first at an ample nitrogen and thereafter transferred to a low but constant nitrogen supply. However, when seedlings are grown first at an intermediate nitrogen supply and then transferred to a low but fluctuating nitrogen availability, the slow-growing species produce more biomass. Thus, these simulations suggest that slow-growing species are better adapted to nutrient-poor conditions in terms of carbon gain, at least when the nitrogen supply fluctuates.

Even though this simulation has not been validated in pot-experiments, it suggests that care should be taken with ecological interpretations of experimental results. Depending on the nitrogen availability during seedling growth and on the type of nitrogen supply

(constant or fluctuating), the simulations show that fast-growing species may produce higher, equal or lower amounts of biomass than slow-growing species. Moreover, these simulation results may provide insight in alternative experimental set-ups. To better understand nitrogen nutrition and its effect on growth in the field, plants also should be grown at fluctuating nutrient availability.

Contribution of maintenance of biomass, growth, and ion uptake to the total rate of respiration continuously shifts under conditions of fluctuating nitrogen supply (Fig. 4A). This means that both the rates of the energy requiring processes and their associated specific respiratory costs should be taken into account when modeling whole-plant growth. At present, special attention should be given to the specific respiratory energy costs for the maintenance of biomass and ion uptake at low nitrogen supply because such costs may be completely different from the values obtained under high nitrogen supply (Van der Werf et al. 1992a, 1994)

Acknowledgment

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Root Activities and Function in Component Crops for Intercropping

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Abstract

Respiration was used as an indicator of root activity and was correlated to nitrogen (N) uptake, using data from field experiments of pigeonpea-based intercropping with sorghum, pearl millet, cowpea, and groundnut.

Respiration rate of an entire root system was obtained from the slope of a regression line betzveen total respiration and weight of roots in a soil block collected by the monolith method. Rates of root respiration decreased as growth stage advanced and was higher in intercropping than in sole cropping. Respiration was separated into growth and maintenance components. Legume components in the intercropping showed a lower conversion efficiency of respiratory substrates into dry matters and a higher maintenance respiration than cereal components. The respiratory energy required by pigeonpea to take up N from the soil and atmosphere was higher than that for other crops.

We concluded that due to physiological adaptation to limited N status, respiratory cost for N-accumulation is much higher in pigeonpea than in the other crop species. Intercropping causes a slight increase in root respiration, probably through alteration in patterns of dry matter distribution.

Introduction

Among various root traits, length and weight are most commonly measured both in the laboratory and in the field because they are closely related not only to carbon allocation to roots but also to the uptake of nutrients and water, which is a major function of roots. Although profile distribution of these characteristics in soil layers is greatly affected by physico-chemical properties of soils, considerable differences exist in root system architecture among plant species and genotypes. Characterization of root systems will become a more reliable source of information for better utilization of water and nutrients if certain physiological activities of roots are measured together with length and weight.

Root respiration is one of the physiological characteristics relatively easy to measure

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even in the field, and roughly reflects activities of functions such as growth, maintenance, and ion uptake. If root respiration can be separated into these components, a more solid understanding of species and genotypic differences from the viewpoint of shoot-root interaction is possible.

In this chapter, root respiration is discussed in relationship to the major function of roots, uptake of nutrients, particularly that of nitrogen (N). For this purpose, first we describe internal and external factors affecting root respiration. We then attempt to separate root respiration into its components using our field data. Finally, we compare respiratory costs for N-uptake among different crop species commonly used for intercropping in the semi-arid tropics (SAT).

Factors affecting root respiration

Root respiration is affected by both internal and external factors. Because the root is a heterotrophic organ, its respiration is entirely dependent on the photosynthetic supply of carbohydrates from shoots. Root respiration rates show a positive correlation with concentrations of soluble sugars in roots (Lambers 1985; Bingham and Stevenson 1993). Therefore, separation of roots from the plant causes a sudden decline in respiration. Moreover, detached roots lose the phenomenom of midnight rise of respiration that is commonly observed in attached shoots and roots as well as detached shoots (Yamagishi et al. 1989). This provides a clear example of the fine control of root respiration by shoots not only in its quantity but also in diurnal rhythms.

Root respiration varies with position on the root axis. In wheat roots, respiration rate was 3-5 times higher in the root tip (0-0.5 cm from seminal apex) than in other parts of the seminal axis (Bingham and Stevenson 1993). In *Agave mapisaga,* roots with laterals showed about a 70% higher respiration rate than roots without laterals. Root respiration per unit dry weight decreases with age (Nobel et al. 1993). Although the morphological differentiation of root tissues is not as great as that of shoot tissues, the root should be considered as a complex organ composed of tissues with a wide range of respiratory activities. When we deal with plant root, the above point should be considered.

Among various environmental factors, temperature has the most immediate effect on root respiration. Root respiration is linearly related with temperature over 10 to 30°C, with a Q_{10} of about 2,5 (Osman 1971). The diurnal fluctuation of root respiration generally follows the daily patterns of root temperature (Palta and Nobel 1989). Weger and Guy (1991) reported that temperature during the growth period has little effect on partitioning of respiratory electron flow between the cytochrome pathway and alternative pathways that drain energy and are considered as a wasteful oxidation of carbohydrates. Temperature independence of alternative pathways makes it easier to estimate carbon losses by respiration under field conditions from periodical measurements of root respiration rates of soil and roots using only temperature response curves and diurnal records of soil temperature (Hall et al 1990).

Although a root has no direct exposure to light, its respiration is drastically affected by illumination. Within 12 min of the exposure of plants to illumination, a marked increase

occurred in root respiration of wheat, and an equally sharp decline occurred soon after removal of illumination from the plant (Osman 1971). The rate of root respiration was about 15% higher during the light period than during the dark period (Szaniawaski 1981).

Soil air composition is mainly determined by the balance between gas exchange through the air path in soil micropores and by the activities of plant roots and microbes. The oxygen (O_2) concentration in the rooting zone is indistinguishable from that in the ambient air under dry conditions. Under wet conditions, however, O_2 concentration at a 20 cm depth rapidly decreases (Matsunaga et al. 1994) and CO_2 concentration at 10 cm depth increases about 7-fold and remains higher than that at the ambient level (Nobel and Palta 1989). Root respiration is irreversibly inhibited by 2% CO_2 ultimately causing the death of cortical cells within 6 h. This would be such a case where root respiration is inhibited by a considerable accumulation of CO_2 rather than by a reduction of O_2.

Respiratory activities are hampered by soil mechanical impedance to root penetration. In wheat, the respiration rate of seminal root tips (0-1 cm zone) is significantly lower in compact soils than in loose soils (Atwell 1990). In hydroponic culture of tomato plants, root restriction causes a 2-3 fold decline in root respiration possibly linked with ethylene production (Peterson et al. 1991).

Nitrogen supply has a relatively small effect on both translocation of assimilated ^{14}C to below-ground and release of ^{14}C from growing roots by respiration and exudation (Johansson 1992). On the other hand, van der Werf et al. (1993) found a higher respiration rate in roots supplied with high N than in those supplied with low N. The rate of root respiration is further increased by the addition of nitrate (NO_3) and ammonium (NH_4^+) into the culture medium (de Visser et al. 1986). Roots supplied with NO_3^- oxidize a lower proportion of carbohydrates through the alternative pathway than those with NH_4^+, indicating that the respiratory efficiency is affected by N species (de Visser 1985).

As expected from the above, root respiration is highly variable due to many factors involved in its regulation. This could be the main reason why many crop physiologists working in this area avoid field measurements of root respiration. As a result, studies have been directed toward the simplification of experimental conditions, that is, greenhouse and laboratory experiments. On the other hand, for the past few decades the characterization of morphological traits of root systems by measuring distribution of root length and weight within soil profile has been extensively carried out in the field. To establish more efficient ways of nutrient management in SAT, we need to increase our knowledge on both morphology and function of roots through physiological studies on root function in the field.

Spatial distribution of root respiration

In a series of experiments, soil blocks were removed from the field using a monolith sampling method to obtain an approximate measurement of root respiration after removal of soils by washing with tap water. In an experiment with pigeonpea and sorghum, the size of each soil block was 10 cm wide, 10 cm deep, and 5 cm high, and the number of the blocks taken from one spot was 54 for sole crops and 108 for intercrops. Total root

respiration found in each block was plotted against root fresh weight in the block. The plot gave a positive correlation with a high regression coefficient (Fig. 1), the slope being the respiration rate (on a weight basis) of the entire root system. Pigeonpea showed a higher rate of respiration than sorghum, and the intercrop had a higher rate of respiration than the sole crop (Fig. 2).

In an attempt to summarize the numerous data, we arranged the root respiration rate representing each block according to the distance from the plant base (Fig. 3). Respiration rate increased with the distance and reached a maximum at about 20-25 cm from the plant base, and then gradually decreased, indicating that the proportion of root tips would be the highest in this region. A similar pattern on the spatial distribution of root respiration in top soil was obtained using datasets from different experiments (Ito et al. 1993).

Most measurements of root respiration have been done with the plants grown in hydroponic culture or pots, and respiration rates ranged from 70 to 300 μmole O_2 gDW^{-1} hr^{-1} (Collier et al. 1993; van der Werf et al. 1993; Poorter et al. 1991). Much lower values are reported from field-grown plants. The root system of *Atriplex confertifolia* was excavated from the field, and root respiration was measured at 12°C in the laboratory (Holthausen and Caldwell 1980). We used an identical method, although the incubation temperature we used was 30°C. The respiration rate ranged from 2 to 15 μmole CO_2 gDW^{-1} hr^{-1}. To explain the disparity in root respiration between laboratory-grown and field-grown plants, Reekie and Redmann (1987) proposed the existence of root dormancy in response to

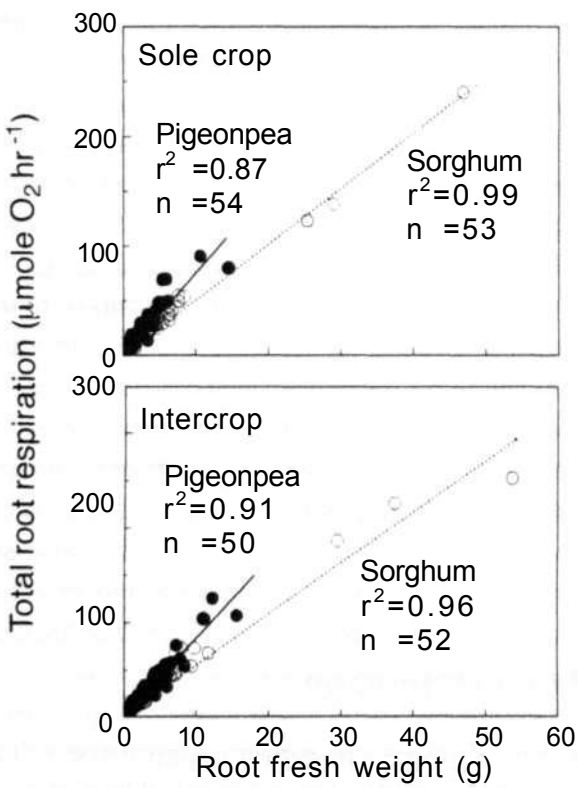

Fig. 1. Total root respiration and root fresh weight measured in a soil block (10 x 10 x 5 cm) taken from the field of pigeonpea and sorghum in sole cropping and intercropping. The slope of the regression lines gives respiration rate on a fresh weight basis.

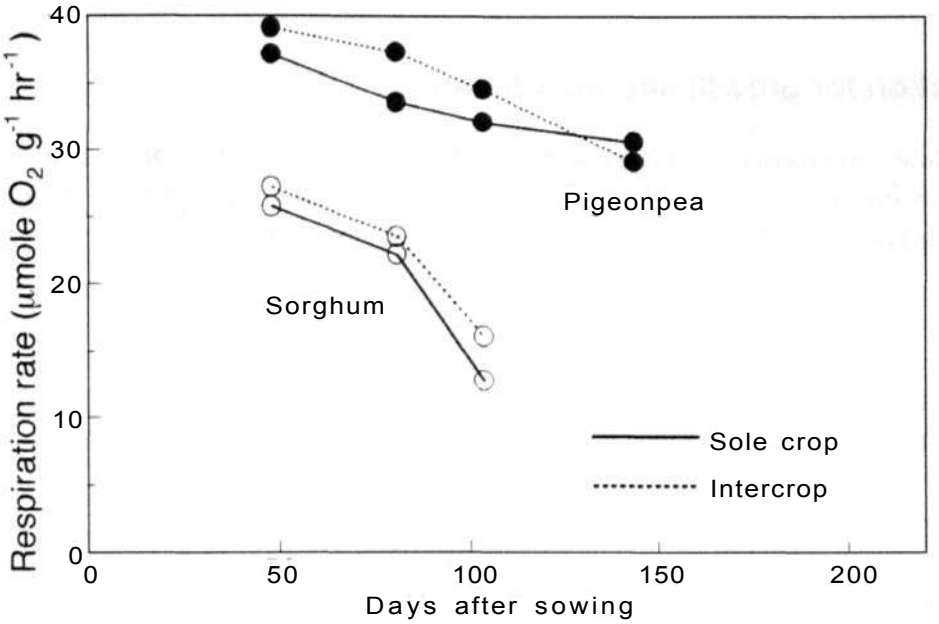

Fig. 2. Respiration rate (dry weight basis) of an entire root system obtained by the regression analysis presented in Fig. 1 in pigeonpea and sorghum under sole and intercropping situation.

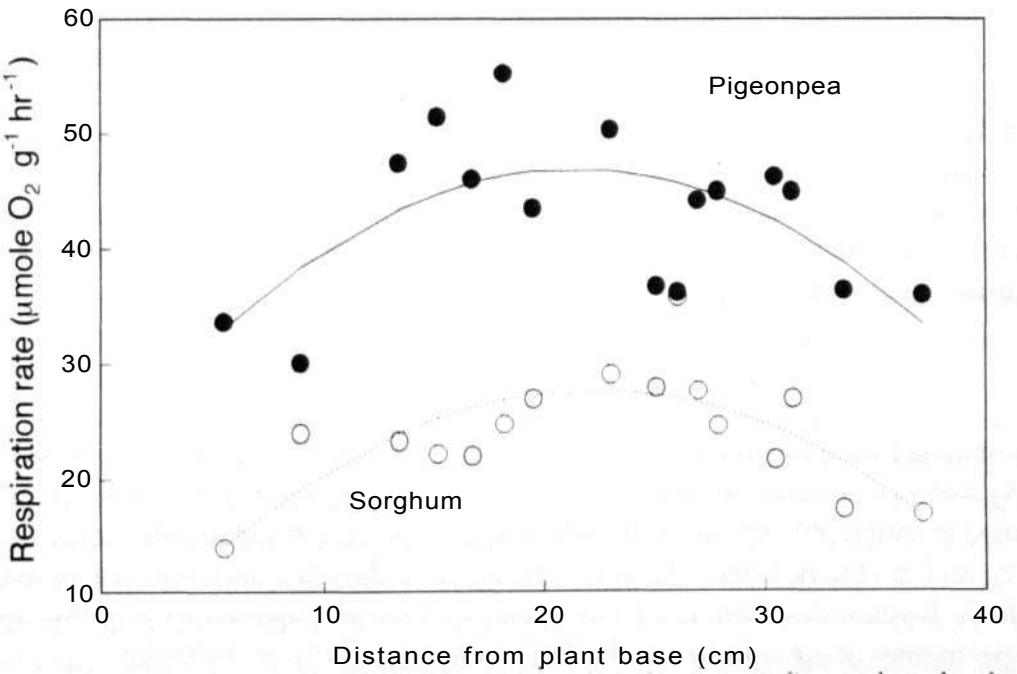

Fig. 3. Root respiration rate (dry weight basis) of pigeonpea and sorghum versus distance from the plant base. Respiration data presented in Fig. 1 were plotted according to the distance between the plant base and the center of the soil block.

environmental stresses that are inevitably imposed on field-grown plants during the growing period.

Respiration for growth and maintenance

To correlate respiratory activities with major physiological function, we separated the respiration into components, such as growth, maintenance, and uptake (Lambers et al. 1983), based on a simple first-order equation proposed by McCree (1970):

$$R = aP + bW, \quad (1)$$

where R is rate of respiration, P is rate of gross photosynthesis, W is dry weight, and a and b are constants. The equation was modified by Thornley (1970) as:

$$R = gdW/dt + mW, \quad (2)$$

where dW/dt is growth rate, g is a growth coefficient, and m is a maintenance coefficient. The g and m were obtained from two-dimensional regression analysis of respiration data with daily photosynthesis of growth rates and accumulated dry matter as the independent variables measured under high and low irradiance. Although this is a relatively easy way to separate respiration into growth and maintenance components, there are situations where great difficulty exists in setting up two different light regimes, especially in the field.

For much easier separation of respiration, equation (2) can be further modified as:

$$R/W = g[(dW/dt)/W] + m \quad (3)$$

where R/W is specific respiration rate and (dW/dt)/W is relative growth rate. The g and m are obtained from the slope and the Y-intercept of the linear regression between relative growth rate and specific respiration rate (Reekie and Redmann 1987). The g is converted to growth conversion efficiency (Yg) which describes an increase in mass of plant material per unit mass of substrate used:

$$Yg = 1/(1 + g), \quad (4)$$

Data obtained from our field experiments were analyzed following this approach (Fig. 4) and Yg and m calculated are listed together with those reported (Table 1). Respiration rates obtained from two different experiments were satisfactorily fitted into the linear regression. The Yg and m obtained here are within the range of the wide variation of reported values (Table 1). Because respiration for ion uptake can not be separated using this approach, changes in rates of ion uptake and variation in the contribution of alternative pathways are speculated to be the main cause of this wide range of reported values (van der Werf et al. 1988).

There is no report on Yg and m for root respiration of field-grown crops as far as we

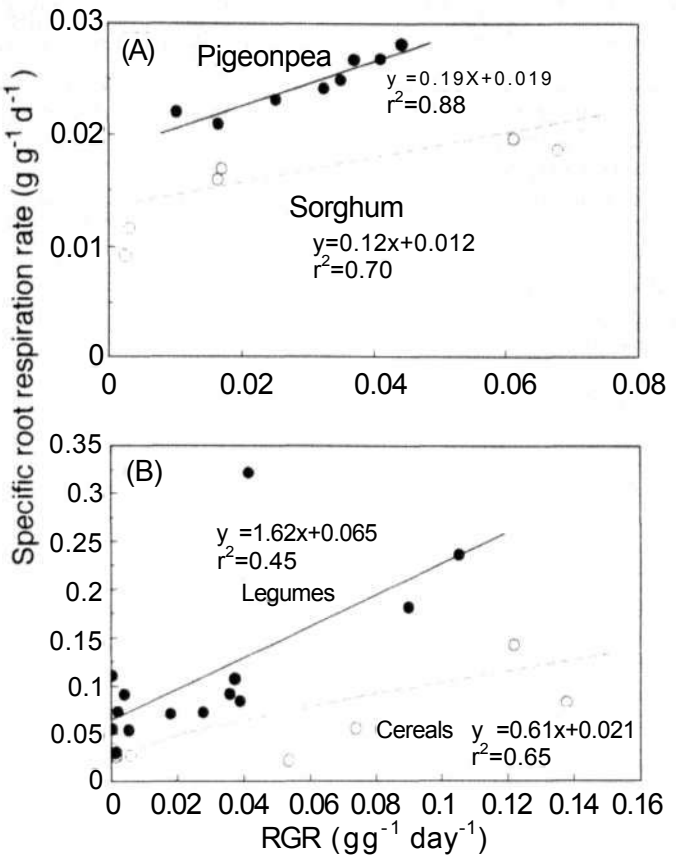

Fig. 4. Specific root respiration rate (dry weight basis) with relative growth rate (RGR) of (A) pigeonpea and sorghum and (B) three legumes (pigeonpea, cowpea, and groundnut) and two cereals (sorghum and pearl millet) in sole cropping and intercropping situation. Conversion factors of O_2 to CO_2 and CO_2 to CH_2O were assumed to be 1 and 0.68, respectively.

know. The relative growth rate (RGR) for roots could not be used for the X-axis of Fig. 4 due to the high variation in root dry mass at each sampling point. Instead, we used the RGR for shoots. Szaniawaski (1981) reported a 1:1 relationship between RGRs for shoots and roots of pine seedlings over time, and Whipps (1987) reported that RGR was similar in roots and shoots of tomato.

Our results showed that to achieve the same growth rate, legumes, including pigeonpea, groundnut, and cowpea, would require a much higher rate of root respiration than do cereals, including sorghum and pearl millet (Fig. 4). In other words, the growth conversion efficiency would be lower in legumes than in cereals (Table 1). In contrast, respiration for maintenance would follow a reverse trend.

A lower Yg is often found in roots compared with that in shoots (Lambers et al. 1983 and Szaniawski 1981). This could be due to (a) the significance of nutrient uptake, (b) more contribution of alternative respiratory pathways, and (c) inaccessibility to photosynthetically derived energy that is exclusively utilized for biosynthetic reaction in green parts of plants. In contrast, however, Hansen and Jensen (1977) reported a higher Yg

Table 1. Growth conversion efficiency (Yg) and maintenance coefficient (m)

Yg	m	Species	Organ	Reference
g g^{-1}	mg g^{-1} d^{-1}			
075	11-15	*Trifolium repens, sorghum bicolor*	shoot	McCree (1970,1974)
0,8	14	*Lolium perenne* L.	shoot	Robson(1973)
0.65-075	20-70	*Hordeum vulgare*	shoot	Ryle et al. (1976)
0.51-052	12-37	*Lolium multiflorum*	shoot	Hansen, Jensen (1977)
0.61-0.64	82-100	*Lolium multiflorum*	root	Hansen, Jensen (1977)
0.81	13	*Pinus silvestris*	shoot	Szaniawski (1981)
0.66	42	*Pinus silvestris*	root	Szaniawski(1981)
0.90	3.6	*Zea mays*	root	Veen (1980)
0.88	9.2	*Carex diandra*	root	van der Werf et al. (1988)
0.71	6.3	*Carex acutiformis*	root	van der Werf et al. (1988)
0.43-078	64-302	14 species	root	Lambers (1979)
0.75	76	24 species	root	Poorteretal. (1991)
0.65	97	*Pisum sativum*	root	Mahon (1977)
0.43	NA[1]	*Plantago major*	root	Dijkstra et al. (1990)
0.67	NA	*Senecio aquaticus*	root	Lambers et al. (1983)
NA	26	*Gossypium hirsutum* L.	shoot	Hesketh et al. (1971)
0.54	37	*Agropyron dasystachyum*	root	Reekie, Redmann (1987)
0.84	L9	*Cajanus cajan*	root	this paper
0.89	12	*Sorghum bicolor*	root	this paper
0.38	65	*Cajanus, Arachis, Vigna*	root	this paper
0.62	21	*Sorghum bicolor, Pennisctum glaucum*	root	this paper

1 NA: not available

in roots than in shoots of *Lolium multiflorum* as shown in Table 1.

The respiratory requirement for maintenance of root systems is usually low (approximately 10% of total respiration) for seedlings of 24 plant species (Poorter et al. 1991) and 8-33 % for maize plants (Veen 1981). Proportion of maintenance respiration increased with plant age (van der Werf et al. 1988). For young seedlings, a requirement of 20-45% has been reported (Poorter et al. 1991). Higher contribution is required for growth respiration.

Respiration for ion uptake

Although ion uptake is a major function of roots, few attempts have been made to separate uptake respiration from other forms of respiration. If the same line of approach mentioned earlier would be followed, the four parameters, growth, root volume, ion uptake, and root respiration, should be measured under different light intensity and after excision of roots. Using multiple regression, Veen (1980) separated respiration into three components: growth, maintenance and uptake. This is rather laborious and can hardly be carried out in field conditions.

The respiratory cost for ion uptake is reported to be about 60% for maize (Veen 1981) and 50-70% for 24 plant species (Poorter et al. 1991). Because ion flow across membranes of epidermal cells is bidirectional, ion efflux is also included in the consideration of respiratory cost. Re-uptake to balance efflux is usually included in the maintenance

component, and up to 73% of the maintenance costs may be for the re-uptake of ions (Bouma and de Visser 1993). Protein turnover, which is another important function for maintenance, accounts for 24-48% of the maintenance cost of roots (van der Werf et al. 1992).

N-accumulation and respiration

We calculated the rate of N-accumulation, including N uptake and N_2-fixation from the difference between two consecutive sampling points, and then plotted this rate against RGR (Fig, 5). A positive correlation was found between the two, however, legumes and cereals fitted different relationships. The result clearly indicates that at the same rate of N-accumulation, cereals can achieve much higher growth rate than legumes. A similar correlation has been reported between rate of N-accumulation (gN m^{-2} d^{-1}) and crop growth rate (g m^{-2} d^{-1}) using eight Gramineae and seven Leguminosae crops (Shinano et al. 1994). They also reported that less dry matter was accumulated in Leguminosae than in Gramineae using the same amount of N.

We calculated the respiratory cost for N-accumulation for each crop used in this experiment (Fig. 6). Pigeonpea had the highest respiratory cost, indicating that pigeonpea requires more respiratory activities to take up the same amount of N. The other four crops, including two legumes and two cereals, show similar values and seasonal trends. This

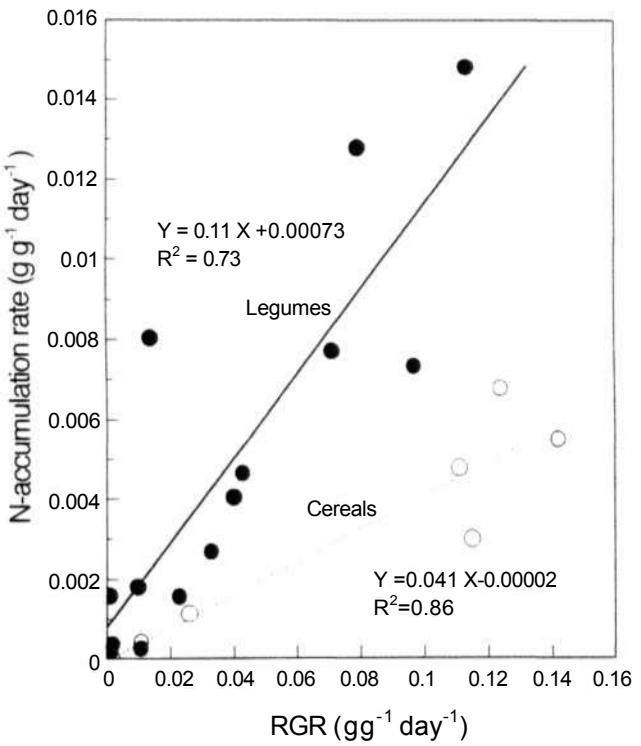

Fig. 5. Nitrogen accumulation rate in plants on the basis of root dry weight with relative growth rate (RGR) of three legumes (pigeonpea, cowpea, and groundnut) and two cereals (sorghum and pearl millet)

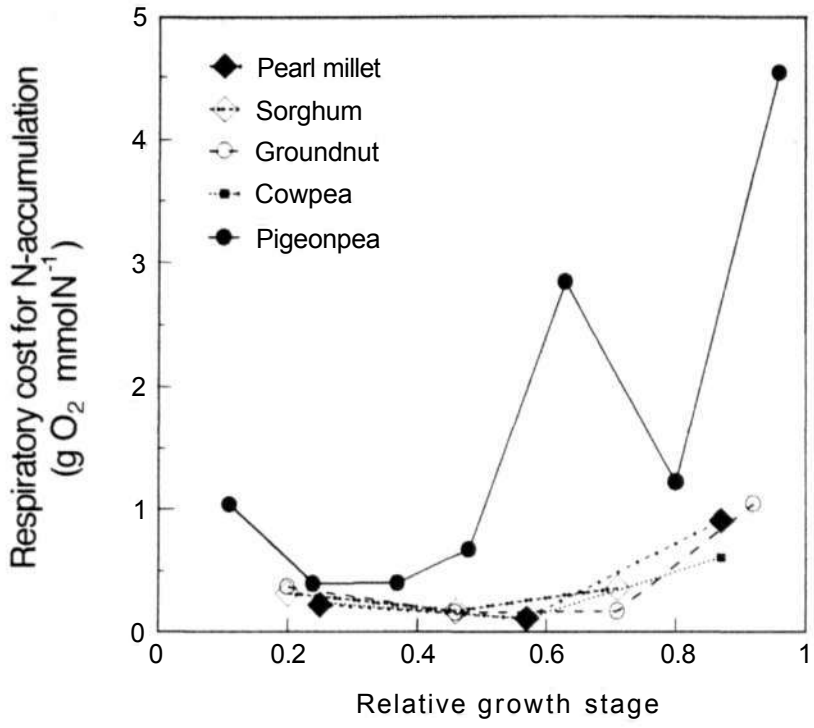

Fig. 6. Respiratory cost for N-accumulation in five crop species with relative growth stage calculated using sampling day/entire growth period.

suggests that a higher respiratory requirement for N-accumulation in pigeonpea may not be due to biological N_2-fixation.

Relatively low values (25-40 mgO_2 mmolN^{-1}) have been reported for respiratory cost by Poorter et al. (1991) and van der Werf et al. (1988). However, 100-400 mgO_2 mmolN^{-1} was also reported for field pea and maize by Mahon (1977) and Veen (1981). The values obtained for four crops, excluding pigeonpea, in our experiment are within this range.

Poorter et al. (1991) and van der Werf et al. (1994) suggested that a considerable difference exists in the fraction of respiration required for anion uptake between fast-growing and slow-growing species. Their data show that the latter plant species require a higher respiratory cost for anion uptake than the former. Respiratory cost for uptake is determined by (a) ratio of ion influx to efflux, (b) proportion of energy-dependent and energy-independent uptake mechanisms and (c) exudation of specific compounds from roots to solubilize ions fixed by soil minerals or humic substances. The pigeonpea used in this study as a main component crop for intercropping requires more than 200 days to reach maturity, far longer than those of the other crops, so it is considered as a typical slow-growing species. A specific compound, pisidic acid, is reported to be released from pigeonpea roots to solubilize iron-bound phosphate that is otherwise unavailable to the plant (Ae et al. 1990). Inherent pereniality and genetic adaption to nutrient-poor conditions might be an inevitable reason for pigeonpea to invest more energy in N-uptake. To have

further confirmation of this finding and supportive evidence for the mechanism behind it, more detailed study should be conducted under controlled conditions.

Conclusion

Although considerable variation exists in respiration data of field-grown plants due to the involvement of various environmental factors in its processes, genetic differences could be still observed among plant species. Legumes and cereals differ in respiratory activities for growth and maintenance of roots. Areas worthy of investigation include whether or not the higher respiratory burden for growth and maintenance in the roots of legumes are related to the formation and function of nodules or morphological differentiation of tap roots. In the relationship of respiration with N-accumulation, pigeonpea showed the lowest respiratory efficiency for N-accumulation. In other words, pigeonpea needs to oxidize more carbohydrates to take up the same amount of N compared with other crops. Pigeonpea is considered a promising component crop in cropping systems of the semi-arid tropics, especially from a viewpoint of adaptability to limited water and nutrient conditions, and soil fertility maintenance. The higher respiratory requirement for N-accumulation by pigeonpea might be a physiological adaptation to stressed environments. This in turn limits yield potential of this crop.

Acknowledgment

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Difference in Root System Development Among Crop Species and Genotypes

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Abstract

The most important subject in the research of crop root systems is to find out how the root growth contributes to dry matter production and ultimately to yield. The reports focusing on this issue are, however, very limited. The purpose of our report here is to correlate root growth with dry matter production and yield. Root systems were quantified and compared for major crops in Japan (*rice, wheat, maize, soybean, sugarbeet, and potato*) *and various genotypes of potato grown in our experimental fields in Hokkaido. Considerable differences were found in various root traits* (*dry weight, length, surface area, and volume*) *at the maximum stage of root growth among the crops and also among the potato genotypes. Among the crops, but not the potato genotypes, these traits showed a positive correlation with shoot* (*leaf and stem*) *dry weight* (*DW*), *but not with total DW and yield. We concluded that an extensive root growth would be necessary to achieve a massive shoot growth during the vegetative growth stage. However, when a storage organ starts to grow, its characteristics* (*e.g., sink size*) *would greatly influence the efficiency per unit root mass, and thus the dry matter production and yield cannot be determined simply with the root quantity.*

Introduction

A concept widely accepted by crop agronomists and physiologists is that size and volume of a root system are important factors in determining plant growth and crop yield through uptake of nutrients and water. A number of studies on crop roots has been published over the past several decades (e.g., Glinski and Lipiec 1990, Kolek and Kozinka 1991, and Waisel et al. 1991). However, the relationship between root growth and yield under field conditions has rarely been a research focus. The role of roots in crop growth and yield is not yet clearly understood, and thus should be further investigated.

A question frequently raised is what is an optimum root size required to maximize dry matter production with adequate absorption of nutrients and water. Siddique et al. (1990) compared the varieties of winter wheat released during the last hundred years in the

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western part of Australia and revealed that an increase in yield was accompanied by a decrease in root weight. Their result suggests that, if the root size exceeds the optimum, the rest of root system may become partly parasitic, resulting in yield reduction.

Our report aims at describing the relationship between root growth and shoot-growth/crop-yield in terms of quantitative measures of root traits made in our field experiments. We first present the difference in various root traits among six major crops; rice (*Oryza sativa*), wheat (*Triticum aestivum*), maize (*Zea mays*), soybean (*Glycine max*), sugarbeet (*Beta vulgaris*), and potato (*Solarium tuberosum*). Then, we explain the difference in root dry weight (DW) among potato genotypes because only scant information is available for this crop. Finally, we describe the relationships of root traits with shoots and harvesting organs among crops and also among potato genotypes.

Root traits

Differences among crop species

Six major crops were compared (Yamaguchi and Tanaka 1990). Rice was grown in a flooded paddy field, and other crops were grown in an upland field at Hokkaido University (brown lowland soil, Typic Udifluvent). Roots were collected with a core sampler (100 cm^3 in volume) until the soil layers that contained visible roots. The collection occurred at about the stage when the shoot (leaf and stem) weight was maximum (maximum shoot growth stage), assuming that the root system had completed its development by this growth stage; i.e., shortly after full flowering (or heading and silking) in cereal crops and potato, initial pod-filling stage in soybean, and mid-August in sugarbeet.

Among the crops there were considerable differences in each root trait (Table 1). The root DW per unit field area was the largest in maize, followed by wheat, rice, soybean, and sugarbeet. The root DW of potato was the smallest, about one-fifth of the largest. The values of the other root traits, except root length, were also smaller in potato and larger in wheat and maize. The simple correlation coefficient (r; * for $P<0.05$, ** for $P<0.01$, and *** for $P<0.001$) of root DW was 0.592 with length, 0.858* with surface area, and 0.953** with volume. The relatively small correlation coefficient between root DW and root length is attributed partly to a larger mean root diameter in maize than in the other crops, and to the different nature of root development among the crops.

The distribution pattern of the root traits throughout the soil layers was also different among the crops (Fig. 1). In rice, a very large quantity of roots was distributed in the top 20-cm soil layer. The percentage of roots distributed in the top 20-cm soil layer (averaged over all root traits) was 45% in maize, 52-53% in sugarbeet and wheat, 62-67% in soybean and potato, and 86% in rice. The soil depth in which 90% of the roots were distributed was shallow in rice (23 cm), intermediate in soybean and potato (35-38 cm), deep in wheat and sugarbeet (48-51 cm), and very deep in maize (59 cm).

In this study, the roots were collected only from the soil layers where the roots were

Table 1. Various root traits at the maximum stage of shoot growth in six crops. (Yamaguchi and Tanaka 1990)

Crop	DW ($g\ m^{-2}$)	Length ($km\ m^{-2}$)	Surface area ($m^2\ m^{-2}$)	Volume ($\times 10^{-1}\ cm^3\ m^{-2}$)	Diameter[1] (mm)
Maize	316	50	88	12.9	0.56
Wheat	247	86	98	9.1	0.36
Rice	203	78	86	7.6	0.35
Soybean	152	39	48	4.8	0.39
Sugarbeet[2]	114	52	64	6.5	0.39
Potato	61	21	22	1.8	0.33

1 Averaged over the whole root.
2 Excluding tap-root system.

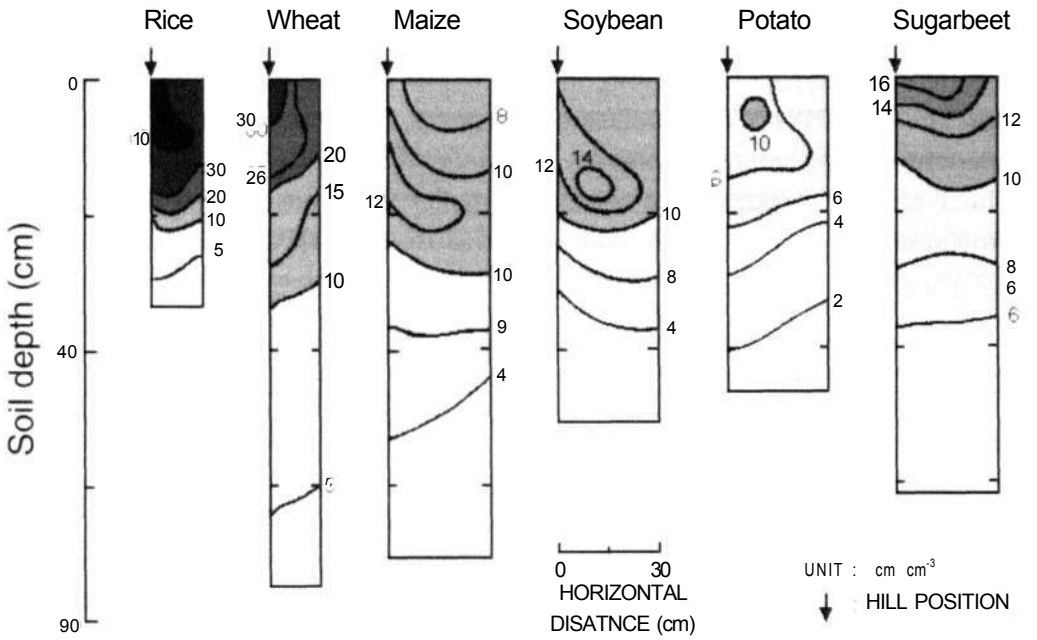

Fig. 1. Distribution pattern of the root length density in the soil profile of six crops shown in Table 1. (Yamaguchi and Tanaka 1990)
Note. Figures denote the root length (centimeter) per unit soil volume (cubic centimeter).

apparently visible, assuming that the roots extending to the deeper layers were not quantitatively significant. The maximum depth of the root system in each crop was estimated by using linear regression on the root-trait density. Estimated depth of the root system was 35 cm in rice, 50 cm in potato, 58 cm in soybean, 69 cm in wheat, 76 cm in sugarbeet and 91 cm in maize. The order and the relative value of these estimated maximum depths of the root system coincided well with those of the soil depth where 90% of the roots were distributed.

Differences among potato genotypes

Twenty genotypes of potato were compared (Iwama and Nishibe 1989). The genotypes are divided into three groups (Table 2): (a) T group, which belongs to *Solarium tuberosum* and is widely cultivated in northern Japan; (b) TW group, which consists of new varieties and lines bred from the crosses between *S. tuberosum* and wild potato species; and (c) W group of wild potato species. Although *S, phureja* and *S. ajankuiri* are cultivated species in South America, they are included in the W group in this classification. The crops were grown at the field of Hokkaido Agricultural Experiment Station (volcanic ash, sandy loam soil). The roots were collected approximately at the maximum shoot growth stage, from the top 30-cm soil layer by the monolith sampling method. In the collection, we assumed that the roots extending to the deeper layers were less than 20% of the whole system at this experimental site (Iwama 1981).

The differences in root DW among the genotypes, especially within the W group, were very large. The root DWs of the smallest genotypes, *S. chacoense* and S. *spegazinii,* were only about one-tenth of the largest genotype, S. *phureja.* Although the differences in root DW within the T and TW groups were relatively smaller than those in the W group, the root DW of the smallest genotype was still one-third to one-half of the largest genotype. A

Table 2. Various root traits at the maximum stage of shoot growth in twenty potato genotypes, including wild species. (Iwama and Nishibe 1989)

Genotype	DW ($g\ m^{-2}$)	Length ($km\ m^{-2}$)	Surface area ($m^2\ m^{-2}$)	Diameterl (mm)	Respiration rate[b] (mgO_2g^{-1})
T group					
Norin 1	16.1	1.7	2.1	0.39	0.90
Benimaru	12.4	1.7	1.9	0.37	1.12
Danshakuimo	9.8	11	1 4	0.39	0.96
TW group					
W822229-1	14.6	1.3	1 6	0.38	0.66
HK 61	11.2	1.4	1.8	0.40	0.94
SK 539	10.7	1.2	1.5	0.40	0.99
R 392-50	9.2	1.2	1.4	0.37	0.57
R 392-25	8.1	0.9	\2	0.41	0.74
Hatsufubuki	7.9	1.0	1.2	0.38	0.97
Konafubuki	7.9	0.9	11	0.39	0.84
WB 66201-10	6.8	0.7	0.8	0.37	0.76
WB 65051-16	5.1	0.6	0.7	0.37	0.89
W group					
S. phureja	40.9	4.9	4.5	0.30	0.72
S. microdontum	21.0	3.9	3.1	0.25	1.06
S. vernei	15.6	2.9	2.3	0.25	0.71
S. commersonii	15.1	2.0	2.1	0.33	0.92
S. stoloniferum	12.9	1.5	1.4	0.28	0.58
S. ajanhuiri	8.4	0.9	1.0	0.33	0.89
S. *chacoense*	4.8	0.7	()7	0.30	0.86
S. spegazinii	3.4	0.4	0.5	0.39	1.12
LSD (0.01)	6.9	0.8	0.7	0.09	0.30

1 Averaged over the entire root system.

2 Means of four detached-root samples with 2-3 adventitious roots having lateral roots.

similar tendency in the difference among the genotypes was also found in root length and root surface area. The simple correlation coefficient of root DW was 0.934** with root length and 0.973** with root surface area. Although respiration rate of detached roots in top 30-cm soils was measured to characterize root quality, the genotypic difference was much smaller in root respiration rate per unit DW than in root DW, length, and surface area.

The difference in root DW among potato genotypes was also investigated using 268 genotypes derived from the crosses between varieties and breeding lines (Iwama et al. 1981). The root DW in top 30-cm soils was measured at the maximum shoot growth stage at our experimental site. There were large genotypical differences from 0.09 g to 5.68 g per plant. In addition, when the genotypes were classified into six maturity classes according to the range of growing period from sprouting to leaf yellowing (maturity class), the mean root DW was larger in the later maturity class (Table 3). A simple correlation coefficient between mean root DW and mean growing period among the maturity classes was 0.991***.

To clarify the effect of soil type on these genotypical differences, four varieties were compared at two sites of different soil types, volcanic-ash sandy-loam soil vs. brown lowland soil (Iwama et al. 1979). At both sites the varietal differences in root DW of top 30-cm soils were clear from a relatively early stage (at almost 30 days after emergence [DAE]) and the order was maintained throughout the growing season (Fig. 2). The relative order in the difference of root DW among the varieties was less affected by soil type.

Interpretation of the results

In the study of crop comparison (Table 1), the total root length per unit field area ranged from 21 (potato) to 86 (wheat) km m^{-2}. The values observed were comparable to or somewhat larger than those reported by other investigators (Table 4). Although the comparison of the values reported by the different researchers may be difficult because of the differences in both the determination methods and growing conditions, the root length is generally larger in gramineous crops (such as maize and wheat) than in the other crops (such as beans and potato). In addition, in the comparison of root traits among genotypes within each crop, O'Toole and Bland (1987) reviewed ample evidence of genotypic

Table 3. Mean root DW in top 30-cm soils at the maximum stage of shoot growth and mean growing period (sprouting to leaf yellowing) within each maturity class in 268 potato genotypes. (Iwama et al. 1981)

Range of growing	68	81	91	101	111	121
period (days)	-80	-90	-100	-110	-120	-145
Maturity class[1]	VE	E	ME	ML	L	VL
Number of genotypes	24	99	41	45	31	28
Mean growing period	76.5	84.9	94.8	105.8	114.6	133.7
(days)	(3.5)[2]	(2.7)	(2.6)	(3.1)	(2.8)	(7.7)
Mean root DW	1.30	1.57	1.77	1.93	2.15	2.77
(8 $pl.^{-1}$)	(0.70)	(0.69)	(074)	(0.71)	(0.78)	(1.18)

1 VE, very early; E, early; ME, middle early; ML, middle late; L, late; VL, very late.

2 The value in parentheses is a standard deviation.

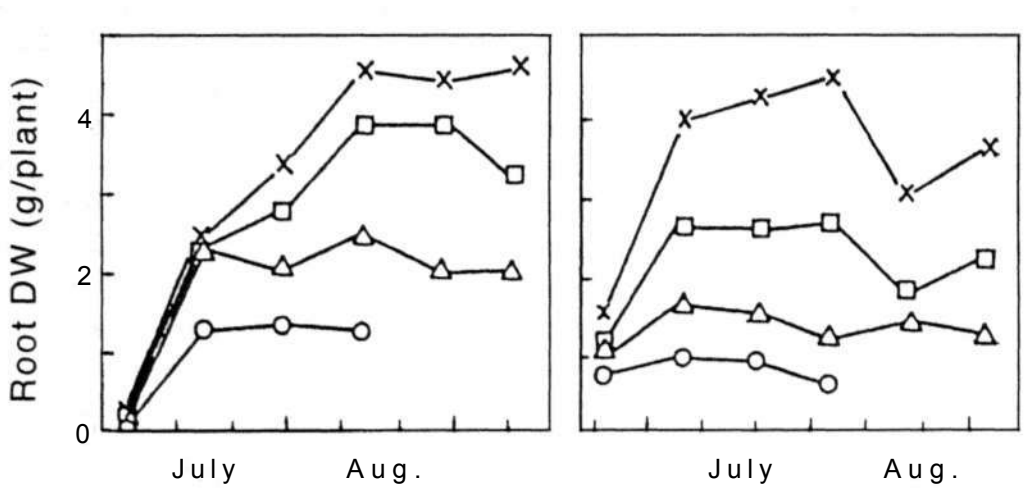

Fig. 2. Changes in root DW of top 30-cm soils of four potato varieties grown in the fields of Hokkaido Univ. (brown lowland soil, left) and Hokkaido National Agric. Exp. Station (volcanic-ash sandy-loam soil, right). (Iwama et al. 1979)

Note. ○ Priekulskiirannii (very early maturity); A Danshakuimo (early maturity), □ Shiretoko (late maturity); X Norin 1 (late maturity).

Table 4. Examples of root length per unit field area in crops reported by other investigators.

Crop	Root length[1] (km m^{-2})	Researcher(s)
Rice	10	Morita et al. (1988)
Wheat	11-23	Welbank et al. (1974)
	20-32	Barraclough and Leigh (1984)
Maize	15	Mengel and Barber (1974)
Pea	5	Greenwood et al. (1982)
Broad bean	2	Greenwood et al. (1982)
Potato	4-7	Vos and Groenwold (1986)
	8-11	Lesczynski and Tanner (1976)
	8-24	Iwama etal. (1993)

1 Variation within the same researcher(s) is derived from varieties, treatments, or experimental years.

differences in many crops, with the exception of potato. Our results of potato demonstrated that there were also large differences in various root traits among the genotypes.

A question to be answered is why these differences in root traits occur among crops and among genotypes. In the comparison of the six crops (Table 1), the root DW at the full development of the root system was the smallest in potato and the second smallest in sugarbeet. Because the storage organs of these two crops (tuber in potato and tap root in sugarbeet) were vegetative, their DW increase started much earlier than those of rice,

wheat, maize, and soybean. In the varieties and breeding lines of potato (Table 3 and Fig. 2), the root DW was smaller in the genotypes of earlier maturity than in those of later maturity. The tuber growth was dependent mostly on maturity classes; the increase of tuber DW started earlier in the genotypes of earlier maturity than in those of later maturity. Generally speaking, allocation of dry matter to roots will drastically decrease when the storage organ starts to grow because it becomes a main sink for dry matter. Our results, therefore, lead to a hypothesis that the differences both in the time and in the extent of the storage organ increase are a main factor affecting the differences in root quantity among the crops and also among the potato genotypes.

Our recent experiment with grafting plants between two potato varieties of different root mass showed that the varietal difference in root DW is mainly due to the inherent dry matter partition to roots and tubers just after tuber initiation (Iwama et al. 1995). The result well supports the above hypothesis.

Root growth versus shoot growth

Comparison among crops

Based on the experiment shown in Table 1, we analyzed the relationships between the root traits and the shoot DW. The shoot DW at the maximum stage of shoot growth was larger in maize and wheat, followed by rice, soybean, and sugarbeet, and the smallest in potato. There was a highly positive correlation between root DW and shoot DW (Fig. 3). The shoot DW also showed high correlation with the root surface area (r=0.858*) and with the root volume (r=0.953**).

These differences in root traits among the crops, however, did not show any close relationships with those in total DW nor with the final yield. At the maximum stage of shoot growth, a simple correlation coefficient between root DW and shoot+storage organ DW was not significant (r=0.425). This is a reflection of a larger DW of storage organs in potato and sugarbeet than that in cereals and soybeans. At the harvesting stage, potato usually has a tuber yield larger than 12000kg ha^{-1} on the DW basis, whereas the yields of wheat and rice rarely exceeds 7000 kg ha^{-1} in our region (i.e., Hokkaido).

Comparison among potato genotypes

In the experiment with 268 potato genotypes (Table 3), we analyzed the relationships between root DW and leaf DW at the maximum stage of shoot growth, and the tuber yield at the harvesting stage. Figure 4 shows that root DW correlated positively with both leaf DW (r=0.800) and tuber yield (r=0.948**) on the basis of mean values of each maturity class. Simple correlation coefficients within each maturity class were also significant between root DW and leaf DW (r = 0.64**~ 0.84**) and between root DW and tuber yield (r = 0.35* ~ 0.49*), with the exception of the L maturity class. The results indicate that an extent of the root growth is associated not only with a shoot growth but also with a tuber yield.

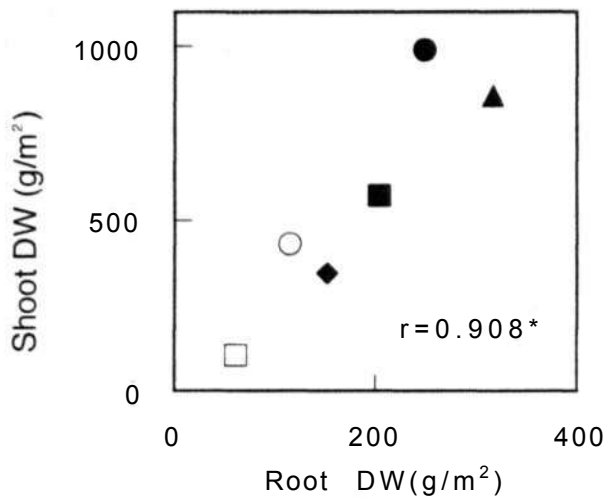

Fig. 3. Relationship between root DW and shoot DW for the six crops shown in Table 1.
Note. ▲ maize; ● wheat; ■ rice; ◆ soybean; ○ sugarbeet; □ potato.

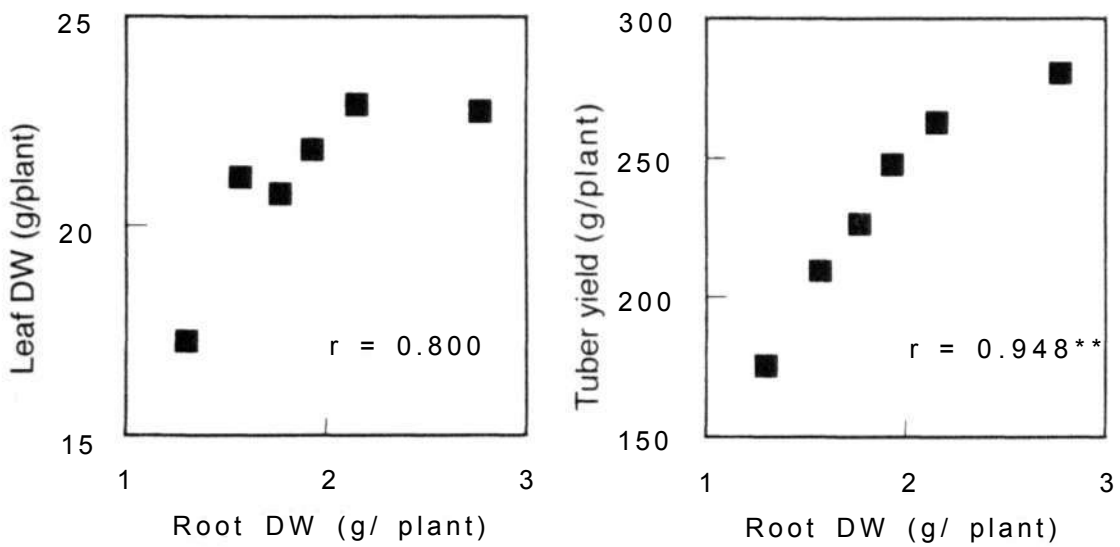

Fig. 4. Relationships between root DW and leaf DW at the maximum stage of shoot growth (left) and between root DW at the maximum stage of shoot growth and tuber yield at the harvesting stage (right) in the mean values of each maturity class shown in Table 3.

In the experiment of 20 genotypes, which included wild species (Table 2), however, the relationships among the traits were somewhat different. The correlation coefficient between root DW and shoot DW was significant among all genotypes (r=0.726***), among varieties and breeding lines (r=0.888***), and among wild species (r=0.722*). On the other hand, as shown in Fig. 5, the correlation coefficient between root DW and total DW was not

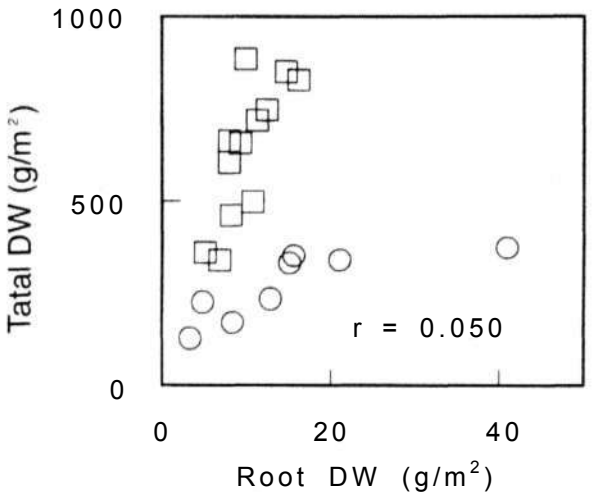

Fig. 5. Relationship between root DW and total DW at the maximum stage of shoot growth among twenty potato genotypes, including wild species, shown in Table 2.
Note. □ T and TW groups, r = 0762**; ○ W group, r = 0785*.

significant among all genotypes (r=0.050), although it was significant among varieties and breeding lines (r=0.762**) and among wild species (r=0.785*). The discrepancy was due to a much smaller tuber DW in the wild species than in the varieties and breeding lines. Because these wild species are sensitive to photoperiod, tuber development started much later in the wild species than in varieties and breading lines under the climatic conditions for the experimental site.

Evidence for the contribution of the amount of roots to the leaf growth and the nitrogen supply to the leaves was demonstrated in a root-pruning experiment (Iwama 1981). Pruning was done at four stages, from 16 DAE to 45 DAE, by cutting the roots (using a flat shovel) 10 cm apart from a hill center perpendicular to and parallel to the row from the ridge top at a 30-cm depth. The percentage of roots pruned by each treatment varied among the dates of the treatment because the proportion of root DW in the soil just beneath the plant changed with an advancement of plant growth. The pruning percentage ranged from 30% (the first treatment) to 44% (the last treatment) on a DW basis . Figure 6 shows that root pruning either reduced the increase of leaf DW at the first and the second treatments or accelerated the decrease of leaf DW at the third and the last treatments during a period of 2 to 3 weeks after each treatment. In addition, each treatment affected the nitrogen concentration of leaves; the concentration in the treated plants fell below that in the controls after the treatments. The tuber yield at the harvesting stage also significantly decreased due to the treatments in the range from 23% (the first treatment) to 40% (the last treatment) relative to the control.

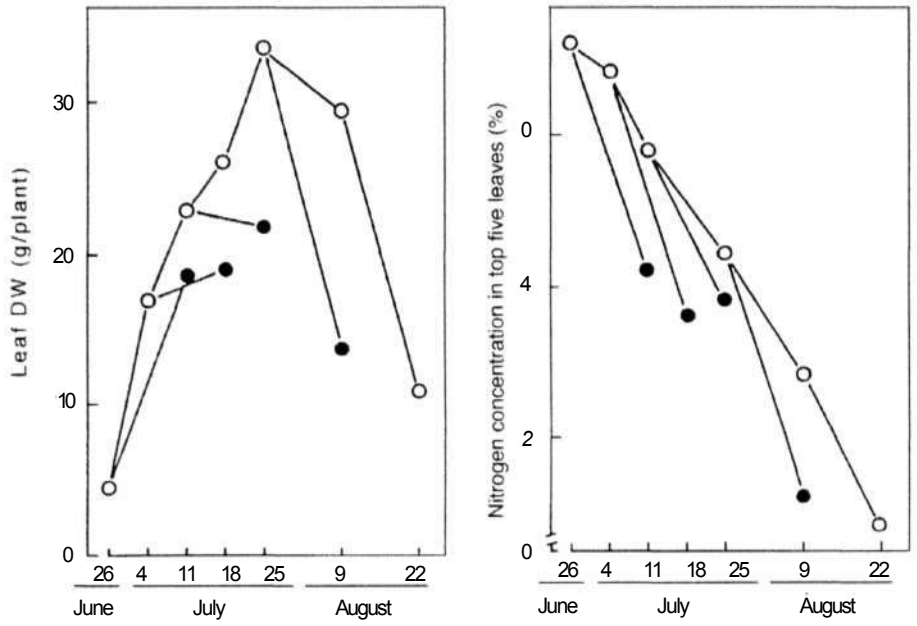

Fig. 6. Effects of root pruning on leaf DW (left) and nitrogen concentration of top five leaves (right) 2 to 3 weeks after the treatments in a potato variety (Irish Cobbler, early maturity) grown in the field of Hokkaido National Agric. Exp. Station. (Iwama 1981)
Note. 0; Control plants; ● Root-pruned plants.

Interpretation of the results

The most important question in these studies is what is the major factor determining the dry matter production and yield, and how the root traits relate to it. In a comparison of all studies presented, the relationship between root DW and shoot DW was highly positively correlated. The root-pruning experiment of potato also showed the great influence of the amount of roots on the growth and nitrogen concentration of leaves. Our results agree with the assumption of Brouwer and De Wit (1969) that there is a close relationship between roots and shoots through the transport of nutrients and water from roots to shoots and also through the transport of assimilates from shoots to roots. An extensive root growth is necessary to produce a large shoot growth.

There was, however, no significant relationship between root DW and total DW nor between root DW and final yield when the six crops were compared. Potato and sugarbeet showed much higher dry matter production per unit root mass than the other crops. This result implies that potato and sugarbeet have a much higher root efficiency for dry matter production and nitrogen absorption than the other crops. We suppose, however, that these higher root efficiencies in potato and sugarbeet are not derived from the characteristics of roots per se, but from the characteristics of the storage organ; the characteristics of the tubers or tap roots enable the roots to absorb nitrogen and the leaves to produce dry matter more efficiently than those in the storage organ of cereals and soybean. The ability of a storage organ plays a key role on the root efficiency for nitrogen absorption and dry matter production.

The result in a comparison of potato genotypes between wild species and

varieties/breeding lines supports the above hypothesis. The wild species showed a much smaller tuber DW, and thus much lower root efficiency for dry matter production than the varieties and breeding lines. The result is apparently due to the restricted tuber growth in the wild species because of their high sensitivity to photoperiod. The small difference in the root respiration rate per unit root mass among the genotypes proves that the lower root efficiency in wild species is not due to the characteristics of roots per se.

On the other hand, in the comparison of potato genotypes among the varieties and breeding lines and also among the wild species, the genotypes with larger root DW had a larger total DW and higher tuber yield. Because the difference in the response of tuber growth to photoperiod is small among the varieties and breeding lines and also among the wild species, the difference in the characteristics of tuber for dry matter accumulation is relatively small. Our results indicate that for a similar ability in the storage organ for the dry matter production, a larger root growth contributes not only to massive shoot growth but also to a larger total dry matter production and a higher yield.

Concluding remarks

A crop or genotype with an active storage organ is able to absorb nitrogen efficiently and to produce larger dry matter irrespective of root quantity. If the activity of the storage organ is similar, the amount of roots is a major factor in influencing dry matter production and yield. Therefore, in crops with small roots but active storage organs, such as potato and sugarbeet, increasing the root growth will be beneficial in increasing the nitrogen absorption, dry matter production, and crop yield. However, in crops such as wheat and rice, an improvement in the storage organ is more important in increasing the yield because of their larger roots but less active storage organ.

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Development of Root Systems in Wheat and Rice

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Abstract

Structure and development of root systems in wheat and rice are reviewed briefly and effects of soil water status on root system growth are discussed. Root systems of wheat and rice consist of seminal and nodal root axes as well as numerous lateral roots. Although root system structure is fundamentally the same in wheat and rice, dimensions and distribution of the root system are different between the two species, possibly reflecting their different strategies for responding to environmental stresses. The dimensions and distribution of root systems are considerably influenced by both genetic and environmental factors. Soil water content is one of the important environmental factors determining root system development. Morphological plasticity occurs through a third factor, the developmental factor, when both genetic and environmental factors operate. One aspect is shoot-root relationship and another is the interrelationships among different components of root systems. Behavior of different components of a root system with respect to environmental factors is not always the same. We examined the effects of soil water status on the grozvth of root components with different dimensions (*e.g., root axis, and large and small lateral roots*) *in wheat and rice. The smaller components showed compensative growth in drought conditions, while the growth of the larger components such as root axis or large lateral roots were sensitively suppressed by the drought stresses.*

Introduction

Because a crop's root system absorbs water and nutrients as well as anchors the plant body, root system development could be a critical factor in determining sustainable agriculture. Therefore, knowledge of root system development is essential for selecting useful management practices in crop production, especially under infertile soil conditions. In this chapter, structure and development of root systems in wheat and rice are reviewed briefly. In addition, effects of soil water status on root system growth are discussed, especially under rainfed conditions.

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O. Ito, C. Johansen, J.J. Adu-Gyamfi, K, Katayama, J. V. D. K. Kumar Rao and T. J. Rego (Eds.), Dynamics of Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics.

Structure and development of root system

Wheat and rice have a so-called fibrous root system (Fig. 1), which is characterized by many nodal roots (Klepper 1992). The structure of their root systems is fundamentally the same. The framework of the root system is built up of seminal and nodal roots (Taylor and Yamauchi 1991). The primary seminal root, originating as a radicle in the embryo of both wheat and rice, emerges first at germination, followed by other seminal roots in wheat. Primordia of nodal roots are initiated and formed in stems (Percival 1921; Kawata et al. 1972; Kawata and Harada 1975) and their emergence proceeds in pace with successive leaf unfolding in wheat and rice (Fujii 1961; Kawata et al. 1963; Klepper et al. 1984).

Seminal and nodal roots in wheat and rice bear first-order lateral roots, and first-order lateral roots produce second-order laterals, and so on (Fujii 1961; Kawata and Soejima 1974). Formation of lateral roots also occurs in sequence with shoot growth in both wheat and rice (Fujii 1961; Klepper et al 1984). Moreover, seminal and nodal roots as well as most lateral roots have root hairs, which are also important components of root systems (Percival 1921; Kawata and Ishihara 1959; Kawata and Chung 1976).

Dimension is an important aspect of root system morphology with reference to function. There is only one seminal root in rice (Fujii 1961), but five to six in wheat (Percival 1921; Fujii 1961). Number, diameter, length, and degree of branching in nodal roots depend on their positions on the stem (Fujii 1961; Kawata et al. 1963; Yamazaki and Nemoto 1986). Because nodal roots successively emerge coincident with leaf emergence, the total number of nodal roots increases with shoot growth (Klepper et al. 1984; Suga and Yamazaki 1988; Li et al. 1993). The total number and total length of nodal root axes increase to reach a

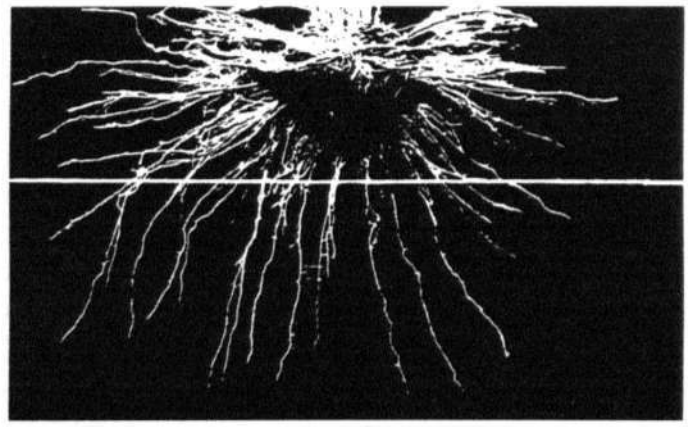

Fig. 1. Root system of lowland rice at the harvest stage. The white lines indicate the soil surface (upper) and plow pan (lower). The depth of the plow pan is 15 cm from the soil surface (Kawata et al, 1963).

maximum value at around anthesis (Brenchley and Jackson 1921; Iwatsuki and Ishiguro 1938). The number of nodal roots in a rice plant at anthesis is several hundred, which is much larger than that in wheat, mainly because rice has more tillers per plant.

Branching degree is very significant with respect to the dimensions of a root system. Because formation of lateral roots also occurs in order with shoot growth, the total root length including any-order of lateral roots also increases and may decrease at later growth stages in wheat and rice (Kang et al. 1994; Morita et al. 1995; Morita and Okuda 1995). Throughout the growing period, especially at the grain-filling stage, lateral roots compose a large percentage of both total root number and total root length in a whole root system (Kawashima 1988; Yamauchi et al. 1987; Kang et al. 1990; Morita and Okuda 1995), which strongly suggests the significant contribution of lateral roots to the function of a whole root system.

Although distribution of root systems also has a possible relation to function, quantitative studies on root distribution are relatively limited. With shoot development, the rooting zone enlarges in wheat and rice (Weaver 1926; Kawata et al. 1963; Gregory et al. 1978). The volume of the rooting zone in wheat is relatively large. Rice, on the other hand, has a shallow and compact root system (Kang et al. 1994; Morita et al. 1995), mainly because of more and shorter nodal roots compared to wheat. The rooting depth in upland rice is often greater than in lowland rice (Morimoto 1940; Hasegawa et al. 1960; Chang et al. 1972), but not as much as wheat, probably due to the short growing period of each nodal root. In both wheat and rice, root weight and root length decrease exponentially with soil depth and most roots are distributed in the upper soil layers, especially at the grain-filling stage. Although deeper roots are relatively few in a whole root system, they play relatively greater functional roles (Rickman et al. 1991; Morita 1993; Terashima et al. 1994).

Structure and distribution of root systems

Because wheat has more seminal roots and less nodal roots compared with rice, the contribution of seminal roots to the whole root system should be significant in wheat. Spatial distribution of the wheat root system, however, has rarely been studied with reference to structure of the root system (Belford et al. 1987). The distribution of a root system in field-grown wheat was examined by the wall-profile method (Bohm 1979) with special reference to seminal and nodal roots (Morita et al. 1993). At the grain-filling stage, a trench was made parallel and perpendicular to wheat rows to record root number density (RND), which is defined as the total number of roots per unit area of soil profile (Fig. 2). The RND in the top 20-cm of soil was quite high and it decreased exponentially with soil depth to reach an almost constant value at 80 cm. About half of the total root number was in the top 20-cm of soil and about 80% was in the top 60-cm (Fig. 3). After the RND was recorded, the wheat plants with their root system on the soil profile were carefully removed, and the length of seminal and nodal roots on main stems was measured. The nodal roots were rarely longer than 20 cm, which indicated that their distribution might be mostly restricted in the surface soil layers, whereas long seminal roots penetrated into deeper soil layers. It can be concluded that the wheat root system at the harvest stage is

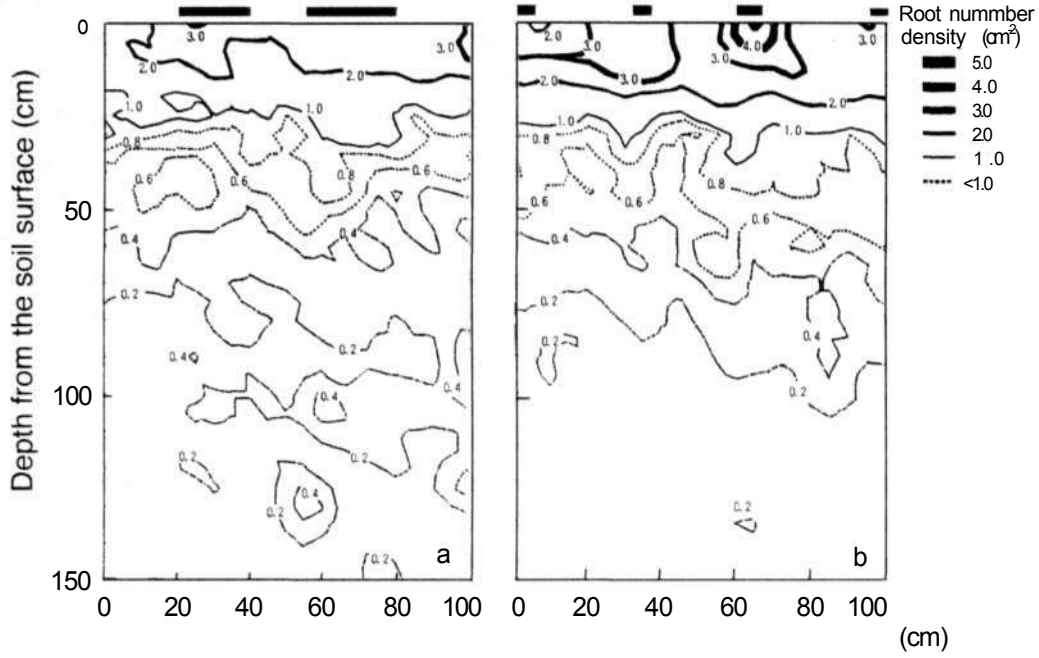

Fig. 2. Spatial distribution of the wheat root system at harvest stage. (a) Parallel to the rows, 1991. Checks on the abscissa indicate where wheat plants existed. (b) Perpendicular to the rows, 1992. Checks indicate the location of rows. The wheat plants were grown at the campus field of the University of Tokyo (Morita et al. 1993).

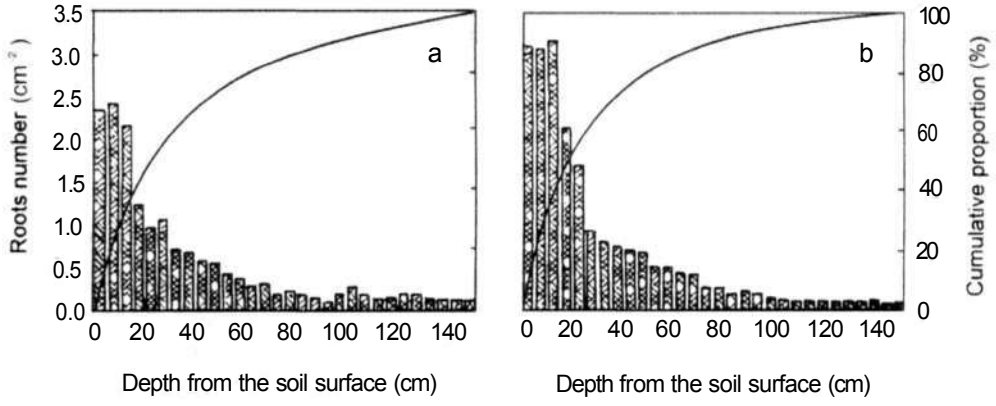

Fig. 3. Average root-number density by soil depth at harvest stage and its accumulation curve. (a) Parallel to the rows, 1991, (b) Perpendicular to the rows, 1992. The wheat plants were grown at the campus field of the University of Tokyo (Morita et al. 1993).

composed of nodal roots confined mainly in the upper soil layers as well as seminal roots extending to deeper soil layers.

In lowland rice cultivation, on the other hand, a seminal root might have a much less significant relation to growth at the grain-filling stage, because seedlings of lowland rice grown under controlled conditions often are transplanted and the root system consists of

many nodal roots that emerge after transplanting. Upland rice, however, is usually directly planted under rainfed conditions. Therefore, growth of seminal roots is important for emergence and establishment of seedlings of upland rice.

Spatial distribution of rice roots has often been studied in lowland rice. Lowland rice has a relatively shallow and compact root system, most of which is distributed in the top 15 -cm of soil (Fig. 1). Because most nodal roots elongate rather straight within the rooting zone, the growth direction of each nodal root can be examined by a cylinder-monolith method (Fig. 4) and analyzed statistically (Abe et al. 1990). One important finding is that rice nodal roots with larger diameter usually elongate more towards a vertical direction (Yamazaki et al. 1981; Morita et al. 1986).

Although information on root system distribution in upland rice is limited, one of the most important characteristics is to extract water from deep soil layers under drought conditions. Rice cultivars with high drought tolerance often have relatively deep root systems (Minabe 1951; Chang et al. 1972; Yoshida et al. 1982). Upland rice often has a deeper root system compared with lowland rice in spite of fewer nodal roots (Hasegawa et al. 1960; Chang et al. 1972), and some roots of upland rice can reach a 70-cm to 80-cm soil depth (Morimoto 1940). The deeper root system in upland rice is probably related to the large diameter of nodal roots (Chang et al. 1972). These roots may permit a higher growth rate and greater branching degree, that leads to a well-developed root system in upland rice compared with lowland rice (Kato et al. 1992; Abe et al. 1994).

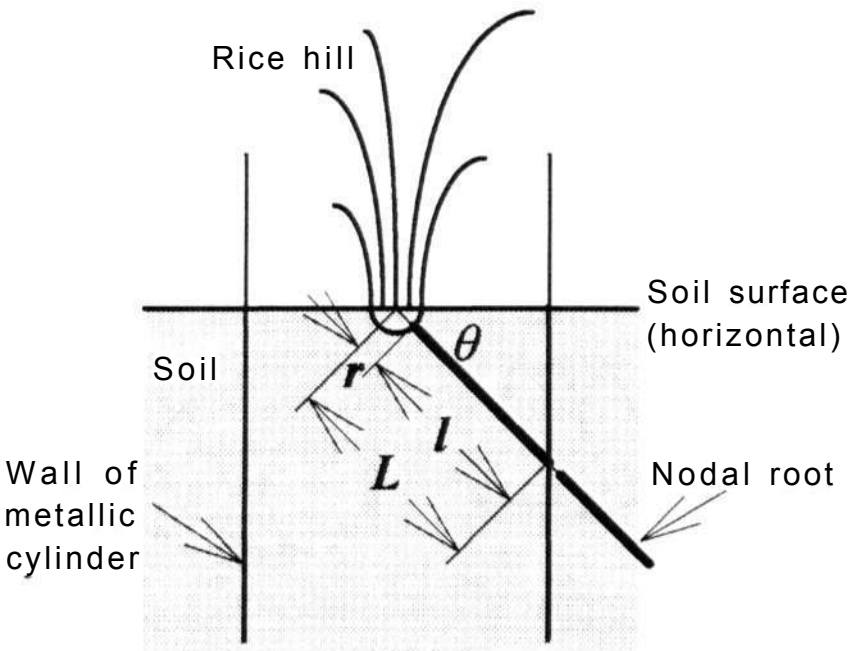

Fig. 4. Estimation of the growth direction of rice nodal roots. θ, growth angle of the nodal root to the horizontal; /, length of the nodal root cut by the cylinder; r, radius of the crown; L, corrected root length ($L = l + r$); R, radius of the cylinder (R = 7.5 cm). The θ can be calculated as θ = arccos(R /L) (after Morita et al. 1986).

Growth and branching of seminal and nodal roots

Our field experiments have shown that seminal and nodal roots of wheat are distributed differently (Morita et al. 1993). Besides, it is already known that seminal and nodal roots are different from each other in timing and position of emergence, and in number and diameter (Percival 1921; Fujii 1961). However, the knowledge of root branching in wheat is very limited (Tennant 1976; Huang et al. 1991). The growth of both seminal and nodal roots in field-grown wheat was examined with special reference to branching (Morita and Okuda 1995). Root system in the top 30-cm of soil was taken using the monolith method (Bohm 1979) at intervals throughout the growing season. The number of seminal roots increased up to five or six soon after emergence and thereafter remained constant. Total length of seminal roots, including their lateral roots, increased with shoot growth to reach a maximum value and then decreased (Fig. 5). Total length of nodal roots with laterals, on the other hand, increased in later growth stages due to emergence and elongation of new root axes rather than branching (Fig. 5), Analysis of the branching index, defined as the total length of lateral roots divided by the total length of root axes (Morita and Collins 1990), indicated well-developed branching in the seminal roots, especially in primary seminal roots (Fig. 6). Thus, total length of seminal roots in a whole root system is relatively high, especially at the early growth stages due to root branching.

In rice plants, nodal root formation proceeds acropetally on each of main stem and tillers, and new nodal roots appear on the third node counting down from the node with an unfolding leaf, as in wheat (Fujii 1961; Kawata et al. 1963; Klepper et al. 1984). The number, diameter, and length of root axes increase remarkably from lower to upper positioned nodal roots during the vegetative phase. Besides, rice forms nodal roots not only on the basal part of the internodes (distal roots), that is, just above the adjacent lower node, but

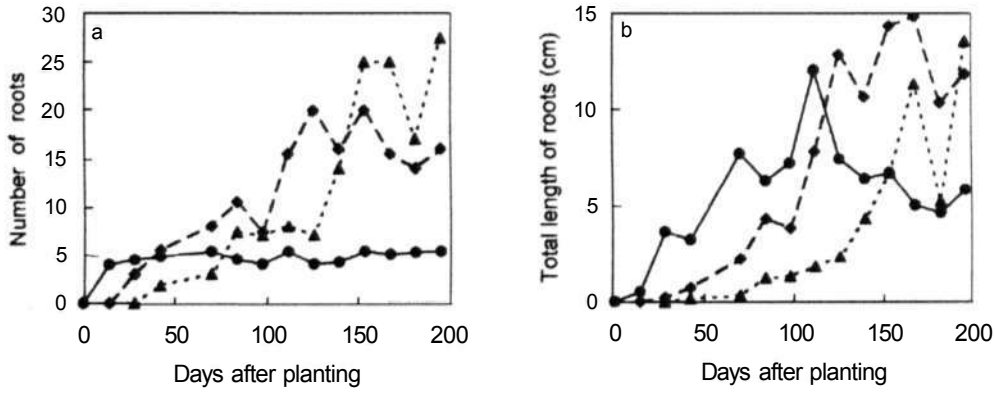

Fig. 5. Development of seminal and nodal roots in a wheat root system. The symbols indicate seminal roots (circles), nodal roots of main stems (diamonds), and nodal roots of tillers (triangles). (a) The number of seminal and nodal roots. (b) The total length of roots including branch roots. The wheat plants were grown at the farm of the University of Tokyo from 1991 to 1992 (Morita and Okuda 1995).

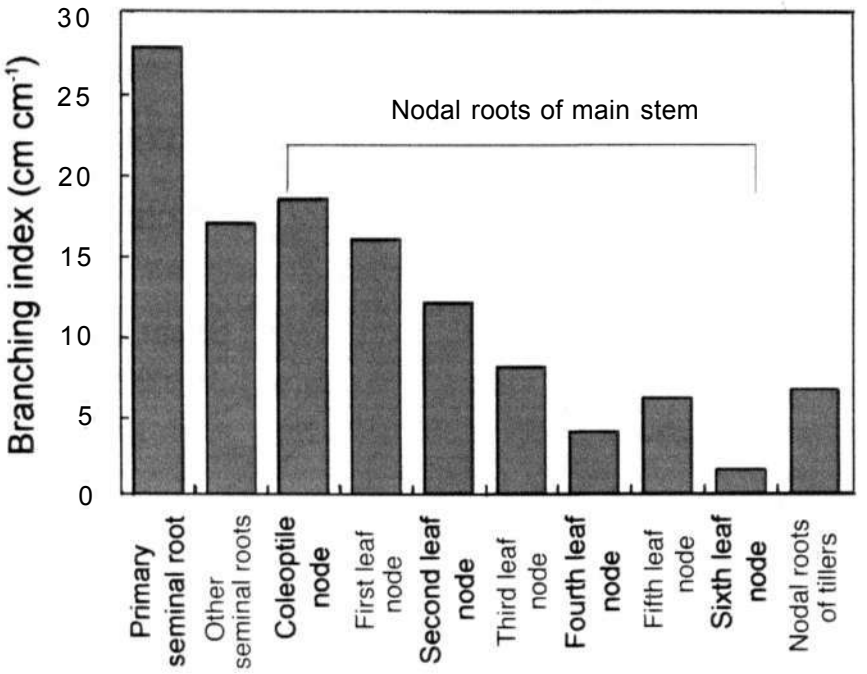

Fig. 6. Maximum branching index of roots in wheat. The wheat plants were grown at the campus field of the University of Tokyo from 1991 to 1992 (Morita and Okuda 1995).

also on the nodes (proximal roots; Fig. 7). This is an another reason why rice has more nodal roots than wheat. The distal roots are thicker and longer than the adjacent proximal roots (Kawata et al. 1963). Moreover, the distal roots with large variation in their diameter grow in various directions depending on both developmental stages and environmental factors, whereas the proximal roots, with small diameter, usually grow horizontally. Furthermore, very thick nodal roots emerging from the most basal part of tillers mostly grow vertically.

Rice nodal roots are often thicker than wheat ones and their branching habit is quite different; rice has more but quite short first-order lateral roots, whereas wheat has less but usually longer laterals. The first-order lateral roots of rice can be classified as thick (around 150 μm in diameter at the base) and thin (about 50 μm) (Kawata and Shibayama 1965,1966; Fig. 8). Rice roots have numerous thin first-order laterals, that are usually less than 20 mm long and form no second-order laterals. The thick first-order laterals are longer and form higher-order laterals, though their frequency is much less than thin laterals. Upland rice usually has well-developed branching roots compared with lowland rice (Kato et al. 1992; Abe et al. 1994) but not as well as wheat. This corresponds with the relative degree of drought tolerance of these crops.

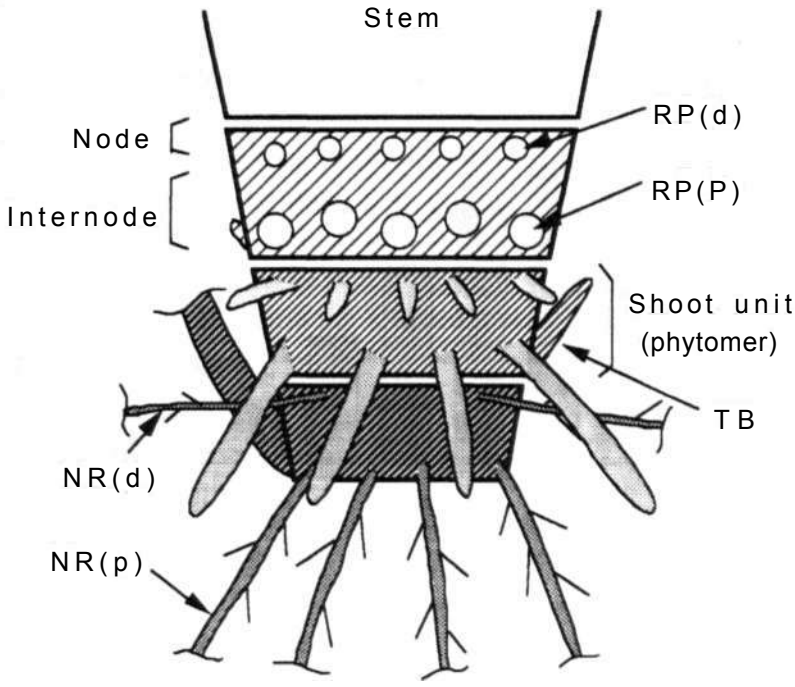

Fig. 7. Schematic of the basic structure of a rice shoot in the vegetative phase. Main stem and tillers are composed of successive 'shoot units' (i.e., phytomer), which develop acropetally. A shoot unit consists of an internode of stem with a leaf at the distal node and a bud of a daughter tiller at the basal site. The leaves of the shoot units are omitted in this illustration. TB, tiller bud; RP(d/p), root primordia of a distal root (d) and a proximal root (p); NR(d/p), nodal root (distal root / proximal root) (after Kawata et al. 1963; Nemoto et al. 1995).

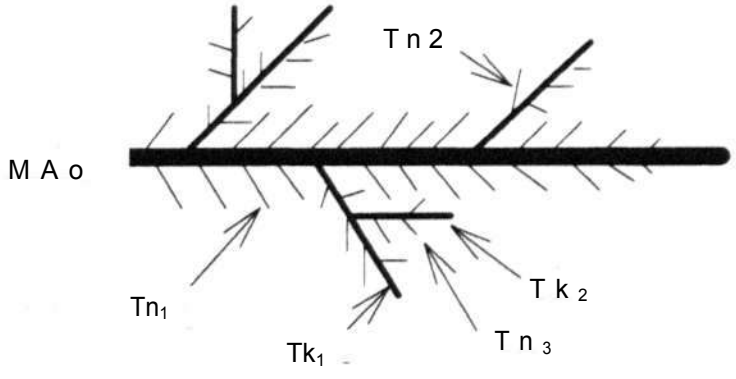

Fig. 8. Schematic of lateral roots of rice. MA_0, main axis of seminal or nodal root; Tk_1, thick first-order lateral; Tn_1, thin first-order lateral; Tk_2, thick second-order lateral; Tn_2, thin second-order lateral; Tn.v thin third-order lateral.

Effects of soil water conditions on root system development

There are two major factors that affect development of root systems: genetic and environmental factors. Although it is well known that there is great genetic variation in morphology of root systems, detailed information is quite limited (OToole and Bland 1987). The discussion here focuses on the effects of environmental factors, especially soil conditions, on root system formation.

Dimension and distribution of plant root systems are much affected by soil conditions, such as soil physical and chemical properties, and temperature (Takeuchi and Hasegawa 1959, Marschner 1986, Iijima et al. 1991). These factors are sometimes closely related to each other, for example, soil impedance and poor aeration as a result of high bulk density.

Soil water status is one of the most significant factors determining the root system development. However, influence of soil water status on root branching has rarely been examined quantitatively. A wheat cultivar, Norin 61, was grown in acrylic tubes with different soil moistures (20% and 30% water content) to investigate the root development with special reference to root branching (Morita and Okuda 1994). The shoot growth of the wheat plants was delayed and suppressed in the dry treatment. The root system was composed of seminal roots with laterals and few nodal roots at 28 days after planting and the root/shoot ratio was increased. The axis of seminal roots was longer in the wet treatments, whereas root branching was more well-developed in the dry treatment. These results suggest the adaptive plasticity of wheat roots to water stress due to root branching.

Our working hypothesis is that a third factor, the developmental factor, should affect root system formation when morphological plasticity is controlled by genetic and environmental factors. The developmental factor refers to integrated and coordinated relationships among growth and development of different organs in a plant. The developmental factor has two aspects: one is a shoot-root relationship and the other is interrelationships among components of a root system; both of these are sometimes compensatory and sometimes competitive. The morphological response of wheat roots to water stress should be under control of a compensatory aspect of the developmental factor.

Influences of soil water content on the elongation of a seminal or nodal root in upland rice have rarely been studied, but varietal differences among rice cultivars in the response to drought at germination has been reported (Kon et al. 1988). The length of seminal roots germinated on filter papers with less moisture was shorter than those on sufficiently moist filter papers, except for Yunnan cultivars, which had the longest and thickest seminal roots. Length of the seminal roots under drought positively correlated with that under sufficient moisture. Elongation of seminal roots in Japanese cultivars of lowland and modern upland rice was suppressed more severely under drought compared with some foreign and old Japanese cultivars of upland rice that form large seminal roots when grown under moist conditions.

Root branching in rice seems to develop more in upland conditions than in lowland conditions (Chang et al. 1972). In upland conditions, soil moisture affects lateral root development (Abe et al. 1994). Upland rice grown under drought conditions increased total root length due to development of longer and thinner first-order laterals. The mean length of thick first-order lateral decreased slightly with low soil moisture content, though the

total number of second-order laterals formed on the thick first-order laterals increased in upland rice cultivars. Thus roots of upland rice respond to drought conditions with an increase in degree of branching degree as do wheat roots, though the responses of the two different types of lateral roots are not always the same. On the other hand, lowland rice cultivars decreased both the mean length of thick first-order laterals and the total number of second-order laterals to some extent under drought condition.

The morphological responses of wheat roots to drought conditions were examined with reference to their functional contribution. Transpiration rate of the wheat plants grown under different soil water conditions (10% - 38% water content) was measured just after rehydration (30% water content in all the plots) at 28 days after planting when root system morphologies including root branching, were different from one another due to different soil water contents (Morita et al. 1994). The wheat plants grown in moderately drought plots (15% and 20% water content) showed higher transpiration rate per unit leaf area than those in well-moistened plots (33% and 38% water content). This high transpiration rate after rehydration was realized by the large ratio of total root length to total leaf area in drought plots due to the well-developed root branching. On the other hand, the transpiration rate was low in severely drought plots (10% water content) in spite of a large ratio of total root length to total leaf area. Low water permeability of the roots may be a reason for the low transpiration rate as hypodermal and endodermal cell walls are often considerably suberized in roots exposed to drought stress (Stasovski and Peterson 1991,1993). These results suggest that the lateral roots developed under drought conditions make a significant contribution to eco-physiological function of a whole root system, though this strategy of adaptation may not be effective under severe drought conditions.

In field conditions, however, not only the total root length but the amount of roots distributed in deep soil layers, where some moisture remains even after drying of the surface soil layers, should be significant. Therefore, tolerance of the root system components of larger size (i.e., seminal roots, nodal roots, and thick lateral roots) to drought may be more important than that of small-sized components (i.e., thin laterals) in some situations, because larger-sized components provide a framework of the whole root system from which smaller-sized components can be distributed in the soil (Yamauchi 1993).

Concluding remarks

Root systems of wheat and rice consist of several components of different size; seminal and nodal roots with first- and higher- order lateral roots (thick and thin laterals in each order). Our working hypothesis is that response of roots to water stress depends on their origin and size; i.e., that growth of larger-sized components, such as the main axis of seminal or nodal roots, is more sensitive to drought conditions than smaller sized-components. Furthermore, when growth of larger components is suppressed by drought, smaller components develop well in compensation. Large components may grow vigorously as an adaptation to drought in species and cultivars that are highly-tolerant to stresses, but wheat and upland rice, moderately drought-tolerant cereal crops, seem to rely more on the

compensatory development of small components (i.e., branch roots) under low soil moisture. Even the small components may be decreased by drought in a sensitive crop like lowland rice.

Acknowledgment

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Root System Development of Component Crops in Intercropping

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Abstract

In India, pigeonpea (Cajanus cajan (L.) Millsp.) has been traditionally grown as a component of intercrops. Identification of a suitable crop combination with different root system architecture to facilitate more efficient nutrient use is required to improve productivity of cropping systems in the semi-arid tropical (SAT) climates. In this study, four component crops, sorghum (Sorghum bicolor (L.) Moench), pearl millet (Pennisetum glaucum (L.) R.Br.), groundnut (Arachis hypogaea (L.)), and cowpea (Vigna sinensis Endl.) were grown either as sole crops or intercropped with pigeonpea. For the measurements of root length and mass, roots were observed non-destructively through minirhizotron observatory tubes with a micro video camera or were excavated by monolith methods.

Although the root length density (RLD) derived using the monolith method is comparable to the estimation of RLD measured using the minirhizotron method, each method best provides estimates of different variables, especially in the soil surface. The total root length (TRL) and RLD for intercropped cereals were unaffected by the cropping system, whereas those for legumes were significantly lowered by intercropping. The reduction was especially significant in pigeonpea before the harvest of companion crops, regardless of the crop combination. However, root development of pigeonpea was improved after the harvest of companion crops. This root development may allow pigeonpea to utilize the residual nitrogen and moisture more efficiently during its later growth stages.

Results of this study suggest that a pigeonpea-based intercropping system provides an excellent way of temporal separation of root systems, and hence would be advantageous in sharing such limited soil resources as nitrogen and water.

Introduction

Growth and development of not only above-ground but also below-ground parts of crops are greatly changed when grown as an intercrop compared with being grown as a sole

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crop. In intercropping the competition for light occurs in the above-ground canopy. Similarly, roots of component crops in intercropping compete for water and nutrients, especially for nitrogen (N), which is in limited supply in most of the semi-arid tropics (SAT). Identification of a suitable crop combination with components differing in root system architecture is one way to facilitate a more efficient nutrient management for improved productivity and N-use efficiency in the intercropping system, but it requires a thorough knowledge of root system development. This is especially important in shallow Alfisols of the SAT, where root expansion is hampered by the hardpan layer and consequently severe competition for N may take place at the soil surface layer.

Although the recent advances in non-destructive methods of root observation using minirhizotron facilities have helped expand our understanding of root system development of individual crops (Upchurch and Ritchie 1983; Levan et al. 1987; McMichael and Taylor 1987; and Vos and Groenwold 1987), few studies have applied it to intercropping research. For field observation of root development, an appropriate method should be carefully chosen, because, each method, even non-destructive methods, has its advantages as well as disadvantages. The main advantage of the minirhizotron method is to monitor root growth and death throughout the growing period (Box et al. 1989; Ferguson et al. 1989; Beyrouty et al. 1990; Cheng et al. 1990; Hendrick and Pregitzer 1992; Heeraman et al. 1993). One disadvantage is quantitative disagreement with the conventional destructive method (Parker et al. 1991; Ball-Coelho et al. 1992; and Benjamin and Sinclair 1994).

In this study, two methods, i.e., non-destructive minirhizotron and destructive monolith methods, were used simultaneously in the field to understand the effects of intercropping on morphological traits of the root systems of each component crop. In addition, quantitative and qualitative comparison was attempted between the two methods.

Comparison of minirhizotron and monolith methods

Conventional destructive methods for root observation necessarily have high coefficients of variation due to location specificity of soil structure and loss of fine roots during the washing process. The minirhizotron technique reported by Upchurch and Rictchie (1983) is non-destructive and allows continuous observations from the same spot at different soil depths. Thus, compared with the monolith sampling method (Majdi et al. 1992), this method is suitable for obtaining time-course changes in root development, though it is not free from location variation that can be reduced only by increased samplings from observation tubes embedded in the soil.

Medium duration pigeonpea (cv. ICP 1-6) was grown as a sole crop or intercropped with hybrid grain sorghum (cv. CSH 5), pearl millet (cv. ICMV 221), groundnut (cv. ICGS 11), and cowpea (cv. IT 82-7D), to simultaneously observe the root development with minirhizotron and monolith methods (Katayama et al. 1995).

The root length density (RLD) of pearl millet, pigeonpea, and their combination decreases exponentially with soil depth (Nakamoto et al. 1989; Ito et al. 1992), suggesting

considerable distribution of roots in the upper soil layer. In general, RLD observed using the monolith method is higher at the 5-cm soil depth than that measured using the minirhizotron method, whereas it is lower below the 15-cm depth. We found that in surface soil layers, ratios of RLD observed using the minirhizotron over the monolith method were below unity, indicating that RLD by the minirhizotron would be underestimated (Fig. 1). On the other hand, the ratios below that layer were above, indicating that the minirhizotron would give an overestimation as compared with the monolith method. Interestingly the fluctuation of the ratios became less, and remained within a narrow range of unity as the growth stage advanced. Underestimation in the surface may be due to effects of light leaking through the top of the minirhizotron tubes above the soil surface (Levan et al. 1987), and to temperature differences at the glass-soil interface (McMichael et al. 1987; Heeraman and Juma 1983; Upchurch and Ritchie 1983; Vos and Groenwold 1987; Majdi et al. 1992). On the contrary, our results showed that the ratios of RLD observed using the minirhizotron over monolith method were above unity below the 10-cm soil layers, indicating that estimations of RLD by minirhizotron were overestimated, as reported by Vos and Groenwold (1987). The present experiment was carried out in a shallow Alfisol with hardpan layer below 30 cm. High bulk densities and subsoil compaction often limit the root profile (Vijayalakshmi 1987). Consequently, roots tend to concentrate at the interface between the soil and tube. Hansson and Andren (1987) showed that in terms of the biomass, the minirhizotron method resulted in a higher relative abundance of roots at the deeper layers than the soil coring method. Recently, artifacts associated with minirhizotron were lessened by using flexible rubber tubes into which positive air-pressure was applied from inside. This resulted in either comparable or higher quality data than that

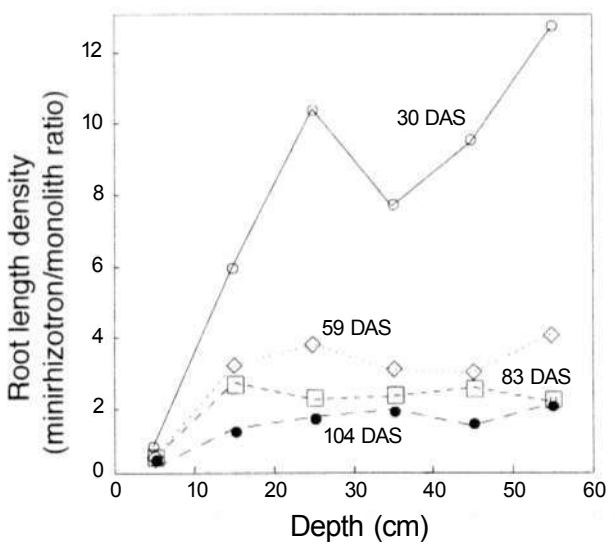


Fig. 1. Ratio of root length density in sole cropping and intercropping observed using the minirhizotron method as compared with that monolith methods at 30, 59, 83, and 104 days after sowing (DAS). All treatments for sole crops and intercrops (A total of 9 treatments) were included together.

obtained using other rhizotron-type devices (Gijsman et al. 1991; Merrill 1992; Volkmar 1993). Another possibility could be that the monolith method gives an underestimation at early crop growth stages. Nakamoto et al. (1992) pointed out that roots of cereal plants can be measured correctly only in situ because such roots are extremely thin and are easily lost during the washing process.

Rooting pattern observed using the minirhizotron method

The quantification of the root system using the minirhizotron method may be problematic due to the artificial environment created at the glass-soil interface. However, this method has an advantage over conventional methods, i.e., developmental pattern of the root system can be followed continuously throughout the growing season at the same spot in the field along the soil profile.

The minirhizotron method was applied to observe the effect of intercropping on the root system of pigeonpea and companion crops. How much detail can be distinguished using this method depends on the spatial and color resolution of the video camera inserted into the minirhizotron observation tubes. Since roots of each component crop in intercropping were difficult to distinguish on the display screen used here, we could only calculate the total root length of both crops. We assumed that the sum of the RLDs of the two component crops in sole cropping was equal to the RLD in intercropping if there was no effect of intercropping. We proposed the following index to evaluate the effect of intercropping;

Intercrop / sole crop ratio = RLD of intercrop / (RLD of sole Pp + RLD of sole Cc)

where Pp is pigeonpea and Cc is a companion crop.

The RLD at the soil surface was reduced by intercropping, except for the pigeonpea/pearl millet combination (Fig. 2). Using the auger method, Reddy and Willey (1981) showed that root density of groundnut/pearl millet combination was smaller than the summation of root density in sole cropping. There was no significant difference in the ratio among three soil layers (15, 25, and 45 cm), regardless of crop combination. Note that the ratio of pigeonpea/cereals was higher than that of pigeonpea/legumes at all sampling points, indicating a greater suppression of root proliferation by intercropping in pigeonpea/legume than that in pigeonpea/cereal combinations.

Rooting pattern observed using the monolith method

Roots of each crop in intercropping can be distinguished visually based on the difference in color, shape, and texture using samples collected by the monolith method after a thorough cleaning and separation of plant debris. This is a great advantage of this method in root research because the effect of intercropping can be examined for individual plant species.

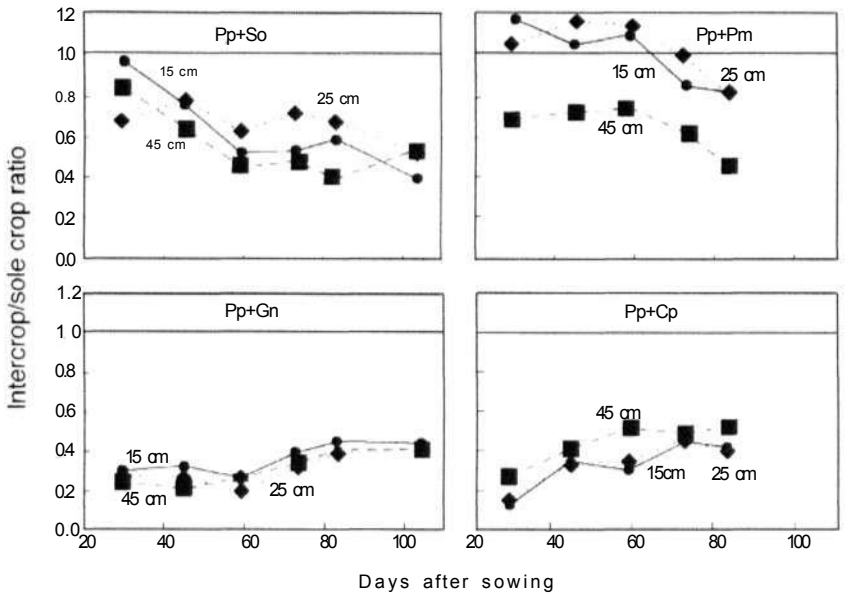
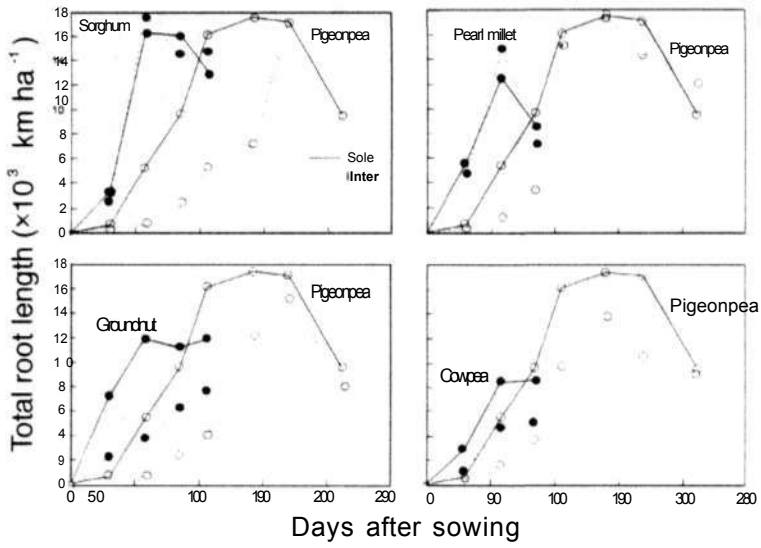


Fig. 2. Ratios of root length density of intercrops as a function of sole crop at 15, 25, and 45 cm soil depth measured using the minirhizotron method.

We found that initial root growth was very slow in pigeonpea compared with that in other crops (Fig. 3). Generally, cereals showed more vigorous root development and a higher RLD at early growth stages than legumes (Yamauchi et al. 1987; Vorasoot 1983; Petrie and Hall 1992). Sivakumar and Salaam (1994) observed that the length of the seminal roots of pearl millet increases exponentially with depth up to 75 days after sowing (DAS).

The total root length (TRL) of intercropped pigeonpea was significantly lower than that of sole pigeonpea at 59 and 89 DAS, regardless of the companion crops. However, there was no significant difference in TRL of pigeonpea in sole and intercrops after harvest of companion crops. In contrast to cereals, the root system of legumes continues to grow even after flowering (Sheldrake and Saxena 1979). We found that root growth of pigeonpea recovered vigorously after harvest of the companion crop except when intercropped with sorghum. This was probably due to lodging. The TRL of groundnut and cowpea was significantly lower in intercropping than in sole cropping at 30, 59, 83, and 106 DAS. However, there was no significant difference in TRL of cereals between sole and intercrops.

The seasonal changes in total dry matter (Fig. 4) were similar with those in root length shown in Figure 3, suggesting that there would be a fine control to maintain the balance between shoot and root growth. The distinct difference in the effect of intercropping between shoots and roots was seen in cowpea where the root extension was markedly reduced by intercropping, whereas shoot development was maintained at the same level between the two. This implies that in cowpea the reduction in TRL by intercropping may not be due to the reduced supply of photoassimilates from shoots to roots. The harvest of companion crops seems to have a more pronounced effect on root growth than on shoot growth, suggesting that there would be a direct interaction in root development between the two crops in intercropping rather than an indirect interaction through a photoassimilate



Fig, 3. Total root length of cereals and legumes in sole and intercrops measured using the monolith method.

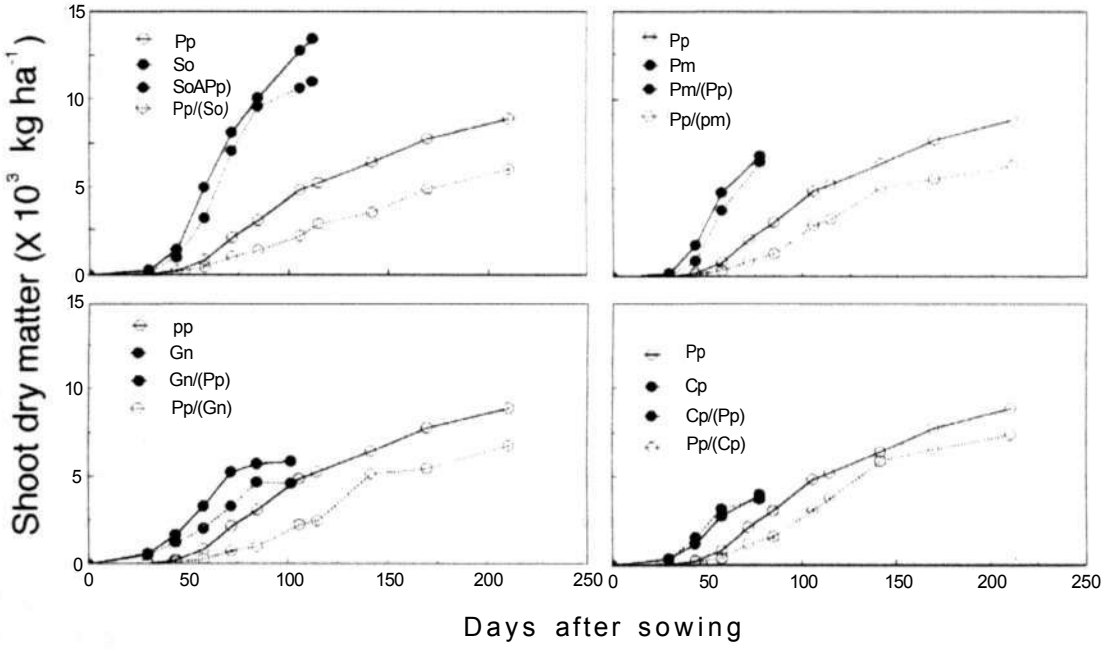


Fig. 4. Total shoot dry matter of cereals and legumes in sole and intercrops.

supply from shoots.

Root distribution across the soil profile showed a characteristic pattern between cereals and legumes, due to the inherent difference in root system architecture (Fig. 5). The RLD of pigeonpea was greatly reduced by intercropping at every soil depth at 59 DAS, regardless of the companion crop. Cereals developed more roots in the soil surface than legumes and

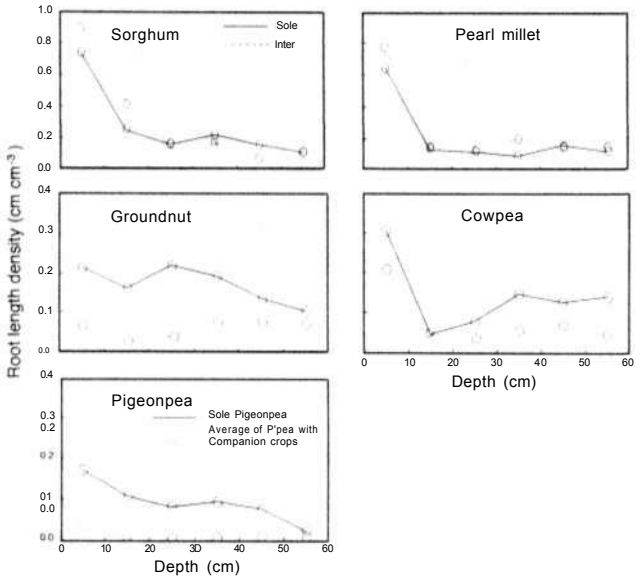


Fig. 5. Root length density of cereals and legumes in sole and intercrops measured by using monolith method at 59 DAS.

spread into the adjacent pigeonpea rows. Polley et al. (1992) reported that root biomass of the C_4 monocots concentrates in the upper 20 cm of soil. Willey and Reddy (1981) observed that leaves of pearl millet in an intercrop with pigeonpea, where soil between the two rows was partitioned by a metal sheet; was yellow compared with those in an intercrop without the sheet, showing evidence of N-depletion from soil under the pigeonpea row by the extending roots. We found that the RLD of intercropped legumes was lower than that of sole legumes. The RLD of intercropped pigeonpea was significantly lower than that of sole pigeonpea at every soil depth, regardless of the companion crop. Pigeonpea has an inherent deeper rooting ability on Alfisols compared with other crops, like soybeans, rice, and maize (Jena and Misra 1988; Arihara et al. 1991). However, due to the presence of a hard stony layer, which consequently confines root proliferation within the surface layer of soil, pigeonpea fails to show any characteristic advantage of root development over sorghum (Ito et al. 1992). High bulk densities and subsoil compaction often limit the rooting profile, thereby restricting the soil use (Vijayalakshmi 1987). This may be closely associated with the reduction of shoot growth (data not shown). The RLD of intercropped groundnut was lower than that of the sole crop at every depth. The RLD of intercropped cowpea was lower than that of sole cowpea at every soil depth, except at 15 cm. In general, the size and number of crown and seminal roots, root weight, degree of root branching and expansion are reduced by competition (Brenchley 1919; Sprague and Farris 1931; Pavlychenko and Harrington 1934,1935). The reduced branching may place pigeonpea at a comparative disadvantage in exploiting water and nutrients. Assuming that the RLDs of groundnut intercropped with pigeonpea and pigeonpea intercropped with cereals and cowpea were reduced by shading from the component crop in our study, our results agree with those of Brouwer and de Wit (1969) and of Demotes-Mainard and Pellerin (1992), who

observed that dry weight of shoot and root of kidney bean and maize is reduced by shading.

Polley et al. (1992) showed that analysis of stable C- and N-isotopes can be used effectively to distinguish roots of species that differ in ratios of ^{15}N to ^{14}N and ^{13}C to ^{12}C Thus, such isotopes can be used to study below-ground competition between or rooting patterns of associated species with different C- and N-isotope signatures. To draw a more realistic picture of root competition in intercropping, the latest methodology developed in root research should be applied.

Conclusion

The RLD obtained using the monolith sampling and minirhizotron methods may be comparable, but we noted that each better estimates distinctly different variables, especially in the soil surface. The monolith method was more reliable in estimating root length of component crops than the minirhizotron method. However, there have been limited studies on root development of component crops in intercropping or mixed cropping, due to the laborious nature of the work. Pigeonpea could be superior in the utilization of resources as nutrients and water that remain after the harvest of component crops because it develops more roots even after flowering. We concluded that pigeonpea-based intercropping systems would be advantageous in sharing a limited resource area, especially in the SAT, through temporal root development of component crops.

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Root System Structure and Its Relation to Stress Tolerance

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Abstract

A crop root system consists of different component roots; mainly a taproot and lateral roots for dicotyledons (dicots), and seminal root(s), nodal roots, and their lateral roots for monocotyledons (monocots). It is important to understand that these root system components are different in origin, age, and morphological and anatomical features. Firstly, we provide experimental evidence for these differences. Such differences strongly suggest that the activities and functions of the different components are also differentiated.

We propose that the root system structure for monocots be defined by the configuration of the root system components in the soil profile, i.e., the extension and direction of nodal roots (framework of the root system) and the development of lateral roots within the framework (network). For dicots, the framework is more simple, but the pattern of lateral root development is more complicated and differs between species.

In spite of the fact that the root system is the organ that is directly exposed to various soil stress conditions, relatively few studies have been conducted on root development under such conditions. We thus present results obtained from a series of experiments that show that the root system structure is closely related to drought and excess moisture (waterlogging) tolerance of the species, for the case of several cereal crops such as rice, finger millet, pearl millet, sorghum, maize, wheat, barley and so on.

Finally, the dynamics of root system development is discussed. We found that the above-mentioned root system components respond to different extents and in different ways to various soil conditions such as soil moisture, mechanical impedance, temperature, allelopathic substances, and nitrogen availability, which consequently caused modification of root system structure. This indicates that phenotypic plasticity varies with component roots, leading to compensatory growth within root systems to facilitate growth and survival of the plant under stress conditions.

In conclusion, a crop root system consists of roots of different nature and the phenotypic plasticity of the root system structure plays a key role in plant expression of stress tolerance.

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O. Ito, C. Johansen, J. J. Adu-Gyamfi, K. Katayama, J. V. D. K. Kumar Rao and T. J. Rego (Eds.), Dynamics of Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics.

Introduction

In an individual plant, different types of roots are produced. When a plant produces morphologically different roots, the phenomenon is called *heterorhizy*. The morphological differences are usually associated with physiological or functional differences. Examples are long and short roots, storage roots, aerial roots, contractile roots and so on. Root nodules and mycorrhizae are also considered heterorhizy. On the other hand, a plant root system generally consists of different types of roots that are actually the component roots, such as taproot and lateral roots for dicotyledons (dicots), and seminal roots, nodal roots and lateral roots for monocotyledons (monocots). The differences among these roots are not as great as those among the heterorhizal roots, hence little attention is generally given to the differences in their morphological and anatomical features as well as their physiological functions.

In this paper, first we will briefly review the nature of such roots to show that plants form a root system consisting of component roots with different morphology, anatomy, and function, in which some of them can also be considered heterorhizy. Then, we will discuss the root system structure as a combination and configuration of these roots, and their functional significance especially in relation to the stress tolerance of crops. Finally, we will present experimental evidence on the effects of several soil stress conditions on the root system structure.

Types of roots

Radicle, taproot and basal root

In seed plants the embryo is bipolar, and in its upper end is the shoot apex and in its opposite end is the radicle. The elongated radicle becomes the taproot (Esau 1977; Zobel 1991; Kumazawa 1980). Therefore, an individual plant has only one radicle by definition. It is unclear, however, when the radicle becomes a taproot.

For monocots, the question arises as to how the radicle is related to *seminal roots* that are frequently referred to in the literature. According to the literature, the number of seminal roots in some cereal crops is one for rice, five to six for wheat, three for oats, three for maize, and nine for barley.

Esau (1962) described the seminal root as one that originates from the primordia formed in the hypocotyl of the embryo of monocot plants. Later, however, Esau (1977) used the terms radicle and *seminal adventitious roots* instead of seminal root. Fahn's description is also similar (Fahn 1990). This means that the term seminal root is not strictly defined morphologically, but refers to all roots that emerge during seed germination; thus the term can be used for monocots. The term taproot is usually used for dicots, but it seems to be applicable also to monocots according to the definition.

It is generally considered that the radicle is a short-lived root, especially for monocots, and would cease to function even in the early growth stages of the plant. However, it is

also known that the radicle continues to function until the later growth stages of the plant, at least heading stage for rice (Kwak et al. 1996a), or sometimes even after heading for several grass species (Weaver and Zink 1945) and for maize (Kauch 1967).

On the other hand, Zobel (1991) defined the seminal roots for dicots as roots that develop from the coleoptilar node or hypocotyl, and are different from the radicle. Furthermore, he ascribed the term *basal root* to the seminal roots excluding the radicle. The basal root originates from the pericycle at the lower part of the hypocotyl or upper part of the taproot (Zobel 1986). This classification is based on Zobel's study showing that the basal root is different ontogenetically and genetically from the radicle, and from adventitious and lateral roots. According to his concept, previously-mentioned seminal adventitious roots or mesocotylar roots that are found in several cereal species can be considered as basal roots (Galamay et al. 1992).

Most root studies, physiological studies in particular, have dealt with either radicles or basal roots. It may be because such roots are relatively easy to work with experimentally. However, it needs to be established if characteristics of these roots are also applicable to other types of roots.

Adventitious roots

Adventitious roots originate from the shoot or subterranean stem. This type of root is sometimes referred to as a *nodal* or *crown root.*

Grazca and Pozsar (1974) found that taproots, basal roots, and lateral roots respond to growth regulators differently. Although adventitious roots differ in origin from the above-mentioned roots, it is still unclear if their physiology and function are also different. Among adventitious roots, it is known that the direction of their elongation is different depending on their position on the stem from where they emerge (plagiotropism), but little is known about other differences, especially about their function. Our limited knowledge on adventitious root function may be attributed to the fact that relatively few physiological studies have been conducted on these types of roots.

With this in mind, some studies were conducted to examine anatomical differences in the adventitious roots of nine species of summer cereals, i.e., rice, finger millet, Job's tears, Japanese barnyard millet, pearl millet, sorghum, foxtail millet, common millet, and maize (Table 1) (Galamay et al. 1991). It was found that the inner structure in the tissue arrangement is similar for the different adventitious (nodal) roots. However, there was one clear difference between the seminal roots (radicle) and the nodal roots. In all species except rice, *cortical sclerenchyma* development was clearly observed in the nodal roots that emerged from the upper stem node at heading, but this development was absent in the seminal roots. In rice, this was observed both in the seminal and the nodal roots. The researchers considered this phenomenon to be a type of heterorhizy.

The cortical sclerenchyma is a tissue of a multi-seriate cell layer that develops in the outer layer of the cortex. Although little experimental evidence has been presented so far, it is supposed that this tissue mechanically supports the structures of the root, protects the root against soil stress conditions and attack by microorganisms, and prevents water leakage.

Galamay et al.(1992) further investigated the developmental process of different axile roots to determine at which root the cortical sclerenchyma development occurs. Specifically, the histological features were examined for the seminal root (radicle), mesocotylar root, coleoptilar nodal root, and the nodal root from the first and second nodes of Job's tears, Japanese barnyard millet, and pearl millet. The results showed that no cortical sclerenchyma development was observed in seminal and mesocotylar roots, but it began to occur in the coleoptilar nodal root in developmental sequence (Fig. 1). In other words, with respect to heterorhizy in relation to cortical sclerenchyma development, the seminal or basal roots and the nodal roots are different types of roots. Research is now in progress in our laboratory to study if these anatomical differences are associated with any functional differences between these roots.

Lateral root

The *lateral root* is sometimes called branch root, but terms are identical. In other cases, the

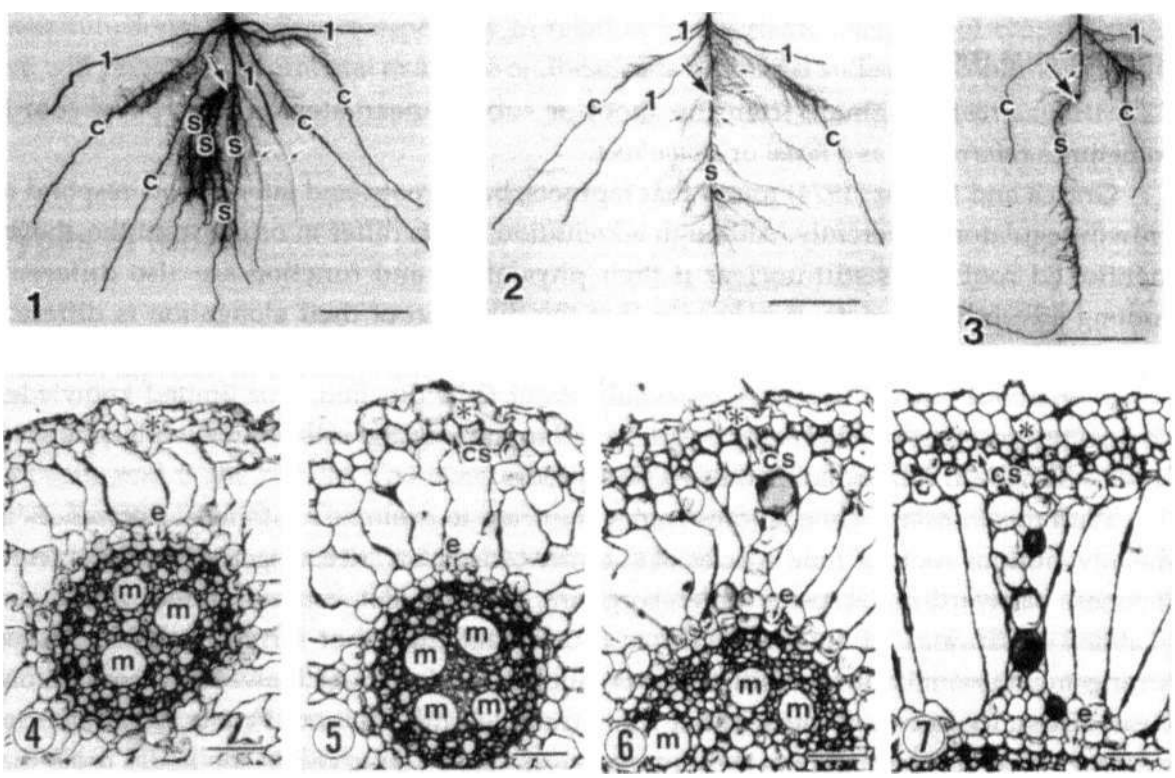


Fig. 1. Root system of (1) Job's tears, (2) Japanese barnyard millet, and (3) pearl millet at the fifth leaf expansion stage. The root system was sampled and photographed using the pin-board root-box method (Kono et al. 1987c). Thick arrows indicate the seed position and small arrows the mesocotylar root. Bar indicates 5cm. c, coleoptilar nodal root; 1, first-nodal root; s, seminal root. Cross-sections *of* (4) the basal part of seminal root, (5) coleoptilar nodal root, (7) first-nodal root, and (6) second-nodal root of Job's tears. Here, cs is cortical sclerenchyma; e, endodermis; m, central metaxylem vessel. Asterisks indicate hypodermis. Bar indicates 100 μm. Note that cortical sclerenchyma is absent in the seminal root (Galamay et al. 1992).

terms "fine root" or "feeder root" are used, but care needs to be taken if they are to be considered as lateral roots.

A lateral root is distinguished from an adventitious root in that the lateral root originates from the pericycle of a parent root. Although lateral roots account for a major part of a root system, in both number and length, little is known about them. Lateral roots in a root system appear to be similar to each other, but it is known that several types of lateral roots exist (Zobel 1986).

McCully (1987) reported that great variation exists in the diameter of lateral roots in a maize root system, and histologically the vascular system in lateral roots with small diameter was apparently simplified. In the case of rice, it is known that there are two types of lateral roots; long and thick roots, and short and slender roots (Juliano and Aldama 1938; Kawata and Shibayama 1965; Kono et al. 1972). Yamauchi et al. (1987a) have designated the first type as L type and the latter, S type. The L-type lateral roots are usually long and thick and are capable of producing higher-order lateral roots, whereas S-type ones are short, slender, and non-branching (Fig. 2).

In the rice plant, these two types of lateral roots are visually distinguishable. The L-type lateral roots show basically identical tissue arrangement with seminal and nodal roots, whereas S-types are anatomically different wherein their vascular systems are simplified.

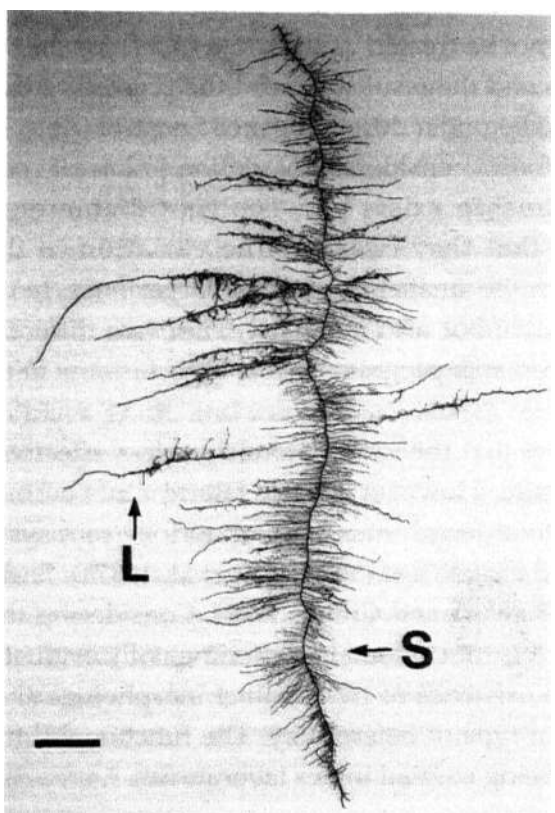


Fig. 2. A seminal root (radicle) system of 1-month-old Jobs tears. Here, L is L-type lateral root; S, S-type lateral root. Bar indicates 5 cm. This root system consisted of 299 L-type and 629 S-type lateral roots, and was 14.2 m in length (Yamauchi et al. 1987b).

These two types of lateral roots also exist in other cereal species (Yamauchi et al. 1987b). In legume species, there are lateral roots that produce higher-order lateral roots and also laterals that do not branch (Kono et al. 1987a). Moreover, there are also lateral roots that cease to elongate a few days after emergence from the parent root, and lateral roots that continue to elongate as the taproot elongates (Mia 1996). It has not yet been examined however, if these morphological and developmental differences are associated with anatomical differences in the inner structure of this particular root.

Generally, a root that is large in diameter elongates to a greater extent, whereas a root with small diameter is short (Cahn et al. 1989; Hackett and Rose 1972). Although this fact seems to be too obvious to mention, it is important to understand this nature of the root.

In the rice plant, for example, Yamauchi et al. (1987a) observed that the average diameter of S-type lateral roots (first-order) that were produced on mature nodal roots of a 1-month-old plant was 80 μm, whereas that of L-type roots was almost double that, i.e., 159 μm. Average length was 7.6 mm for S-type and about 30 mm for L-type. The S-type laterals were almost similar in length, and only very few S-type laterals exceeded 10 mm in length. The L-type laterals varied greatly in length and some of them elongated to more than 300 mm. In other species of cereals (e.g., maize, rye, common millet, Job's tears), although the absolute values for these parameters were different from those of the rice plant, the characteristics of S- and L-type laterals were basically similar (Yamauchi et al. 1987a,1987b). As such, the morphological differences between the two types of lateral roots were very clear so that they should not be treated as the same roots. A genetic analysis was made for the two lateral root types and the results showed the possibility that the initiation of these two types of laterals could be under different genetic control (Kato 1992).

Varney et al. (1991) found considerable variation in lateral root morphology of maize and that a close relationship exists between root diameter, length, and vascular arrangement. It seems that they consider the variation in these parameters to be quantitative, ranging from the smaller ones to the larger ones. In contrast, we believe that the difference is quantitative but also qualitative, i.e., two different types of lateral roots exist in a root system. A research program on this aspect is now in progress to assemble the experimental evidence.

Zobel (1991) indicated that the small laterals are less effective in water and nutrient uptake than even root hairs. However, S-type lateral roots account for 94% of the total number and 75% of the total length in a 1-month-oldrice root system, and 93% and 63%, respectively, in maize of the same age (Yamauchi et al. 1987a). Besides, S-type lateral roots also produce root hairs (Kawata and Chung 1976). Considering these facts, therefore, the functional significance of this root should be experimentally evaluated.

We also consider the existence of two distinct morphological types of lateral roots in the plant root system, as a type of heterorhizy. The functional differences associated with this heterorhizy are now being studied in our laboratory.

Characterization of root system structure

We propose that root system structure be defined by the development of component roots

as expressed by several parameters, such as number, length, diameter, and their configuration in the soil profile.

The importance of root system structure is particularly recognizable when its significance in relation to its function is clearly identified. It was Bray (1954) who first proposed a concept that stressed the significance of root system structure in nutrient and water uptake. This concept pointed out that the root system structure consists of a *root system sorption zone* and a *root surface sorption zone*. The former zone expresses the extension of the root system and is almost equivalent to what is called the "rooting zone". The latter zone indicates the size (area) of soil-root interface, i.e., total surface area of the root system.

For uptake of water and mobile nutrients, because their concentration and total amount in the soil greatly affects crop growth and development, the size of the root system sorption zone is of major functional significance. On the other hand, for the less mobile nutrients like phosphorus, the main factor that controls crop nutrient uptake is the size of the root surface sorption zone. In cereal crops, for example, the size and structure of the root system sorption zone is mainly determined by the length and elongation direction of seminal and nodal roots. In a root system there are very few component roots that show strong positive gravitropism. In fact, most of the roots elongate obliquely at various angles, which is an important consideration in constructing an effective root system network. However, this fact seems not to have been widely recognized. On the other hand, for the root surface sorption zone structure, lateral root development is the key factor. Based on the well-known work of Dittmer (1937) with 90-day-old winter rye root systems, more than 99% of the length and surface area of the entire root system was accounted for by the lateral roots. Yamauchi et al. (1987a) examined the root system of 1-month-old rice and maize, and found out that lateral roots were responsible for 96% of the total root length and 77% of the total surface area for rice, and 95% and 88%, for maize, respectively. For rice plants at maturity stage, the ratio was 97% of the total root length and 76% of the surface area (Kawashima 1988). This trend is more evident in a taproot system; in a 32-day-old soybean plant root system lateral roots accounted for 99% of the total root length and 98% of the total root surface area (Kono et al. 1987a). For other legume species, such as chickpea, cowpea, grasspea, lentil, black gram, and mung bean, lateral roots were also found to be the major component root in their root systems (Mia 1996a).

In this respect, it could be interpreted that the seminal, nodal and taproots build up a framework, and the lateral roots construct a finer root system network. It is easily understood, therefore, that each component root shows different plagiotropism and is quite important in the structural development of a root system. It can be speculated further that in a crop root system, the lateral roots are substantially responsible for water and nutrient uptake as was shown by Varney and Canny (1993), whereas the axile (seminal, nodal, tap) roots are the ones responsible for the effective distribution of the lateral roots in the soil, and conductance of the absorbed and synthesized substances to the shoot.

Significance of root system structure in drought and excess moisture tolerance

Characterizing the root system structure of cereal plants

Based on the idea of root system structure explained above, we attempted to characterize the root system structures of 13 species of cereals (9 species for summer cereals and 4 for winter cereals (Table 1) (Yamauchi et al. 1987b). For this purpose, we used a modified root-box method that has been developed in our laboratory (Kono et al. 1987c). This is a combination of the root-box and pin-board methods that includes different procedures from filling-up the box with soil to photographing the sampled root system. This method allows the intact sampling of an entire root system in an undisturbed two-dimensional condition with negligible injury and loss of component roots.

In this experiment, the summer cereals were raised for 30 days, and winter cereals for 126 days. These periods were sufficient for all the root systems to fill the root boxes (25 x 40 x 2 cm). The root systems were sampled, and then their structures were evaluated based on: (a) direction of seminal and nodal root elongation (rooting angle between plant axis and root), and (b) number, length, and surface area of seminal, nodal, and lateral roots.

The results showed that substantial genetic variation exists in root system structure, and could be generally classified into two major types. One type of root system developed a greater number of nodal roots with relatively small rooting angle. Nodal roots were therefore densely distributed in the soil profile that resulted in relatively small rooting volume. These nodal roots, in turn, developed lateral roots densely, many of which were short and slender (S-type). Examples of crop species that formed this type of root system (designated as *concentrated-type)* were rice, finger millet, and Japanese barnyard millet.

The other distinct type of root system was designated as the *scattered-type,* where fewer but longer nodal roots were developed, many of which elongated obliquely in the soil profile (larger rooting angle). The distance between each nodal root was much greater, which resulted in a relatively large rooting volume. The rooting density of lateral roots was also lower than that in the concentrated-type root system. Among the lateral roots, long

Table 1. Crop species used in a series of experiments described in this section.

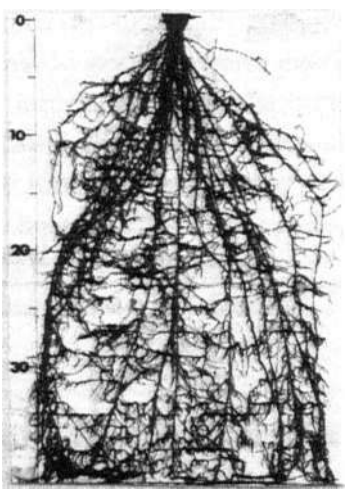
Rice	*Oryza sativa* L.
Finger millet	*Eleusine coracana* Gaertn.
Japanese barnyard millet	*Echinochloa utilis Ohwi* et Yabuno
Common millet	*Panicum miliaceum* L.
Foxtail millet	*Setaria italica* Beauv.
Pearl millet	*Pennisetum typhoideum* Rich.
Sorghum	*Sorghum bicolor* Moench
Maize	*Zea mays* L.
Job's tears	*Coix lacryma-jobi* L.
Barley	*Hordeum vulgare* L.
Wheat	*Triticum aestivum* L.
Oat	*Avena sativa* L.
Rye	*Secale cereale* L.

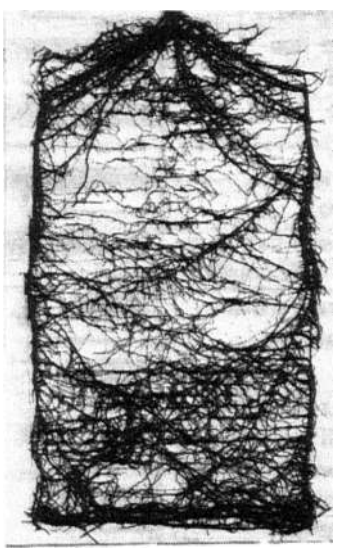
and thick ones (L-type) were predominant and branched into higher-order lateral roots than the concentrated-type (e.g., up to the third order for rice and the fourth order for maize). These lateral roots of different orders were distributed in a relatively large soil space between the nodal roots. Examples of crop species that developed scattered-type root systems were maize, sorghum, pearl millet, barley, wheat, rye, and oat.

Figure 3 shows the summary data for certain root parameters of the root system of rice (concentrated-type) and maize (scattered-type) sampled using the root-box pin-board method.

Drought and waterlogging tolerance

Although plant response to different soil moisture conditions has been extensively studied, we still find some conflicting descriptions about plant tolerance to limited and excess soil moisture conditions (Kono et al. 1987b). In view of this, a series of pot experiments was conducted to quantitatively evaluate the tolerance to both drought and waterlogged conditions of the same cereal species for which the root system structures were studied (Kono et al. 1987b; Yamauchi et al. 1988b). The evaluation was based on dry matter production and yield of each crop when grown under drought (water added weekly or twice weekly to the pots to bring the water content to approximately 22% of maximum water holding capacity), waterlogged, and moderate soil moisture (approximately 62% of maximum water holding capacity) conditions.





	Rice	Maize
NRNo.	29	17
TRNo.	42423	11645
TRL	177.8	130.1
TRSA	0.058	0.122

Fig. 3. Root system of 30-day-old rice (concentrated-type) and maize (scattered-type). The root systems were sampled and photographed using the root-box pin-board method. Scale is in centimeter. Here, NRNo. is nodal roots number; TRNo., total root number (including lateral roots of different orders); TRL, total root length (m); TRSA, total root surface area (m^2) (Yamauchi et al. 1987a and b).

The results showed that the crop species that produced more dry matter and gave higher yield under waterlogged conditions than under drought conditions included rice, finger millet, Job's tears, Japanese barnyard millet, and hulled barley (relatively waterlogging tolerant). A reverse trend was evident for common millet, sorghum, maize, naked barley, wheat, rye, and oat (relatively drought tolerant) (Fig. 4, but data for the winter cereals are not shown). As a result, we found a quite interesting relationship between the type of root system structure of the crops and their drought and waterlogging tolerances, which is suggestive of their functional significance. In general, the crops with waterlogging tolerance showed a concentrated-type root system, whereas those with drought tolerance had a scattered-type root system (Fig. 4).

Crops with a scattered root system seem to have a larger root system sorption zone and consequently have a higher capacity for nutrient and water collection under dry soil conditions. In dry soil, because the mobility of water and nutrients are low, it is imperative that the plants form a large root system sorption zone. On the other hand, the concentrated-type root system has a large number of short and slender lateral roots that permit a larger root surface sorption zone than the scattered-type root system that has rather thick and long component roots. These characteristics seem to be advantageous for intensive nutrient

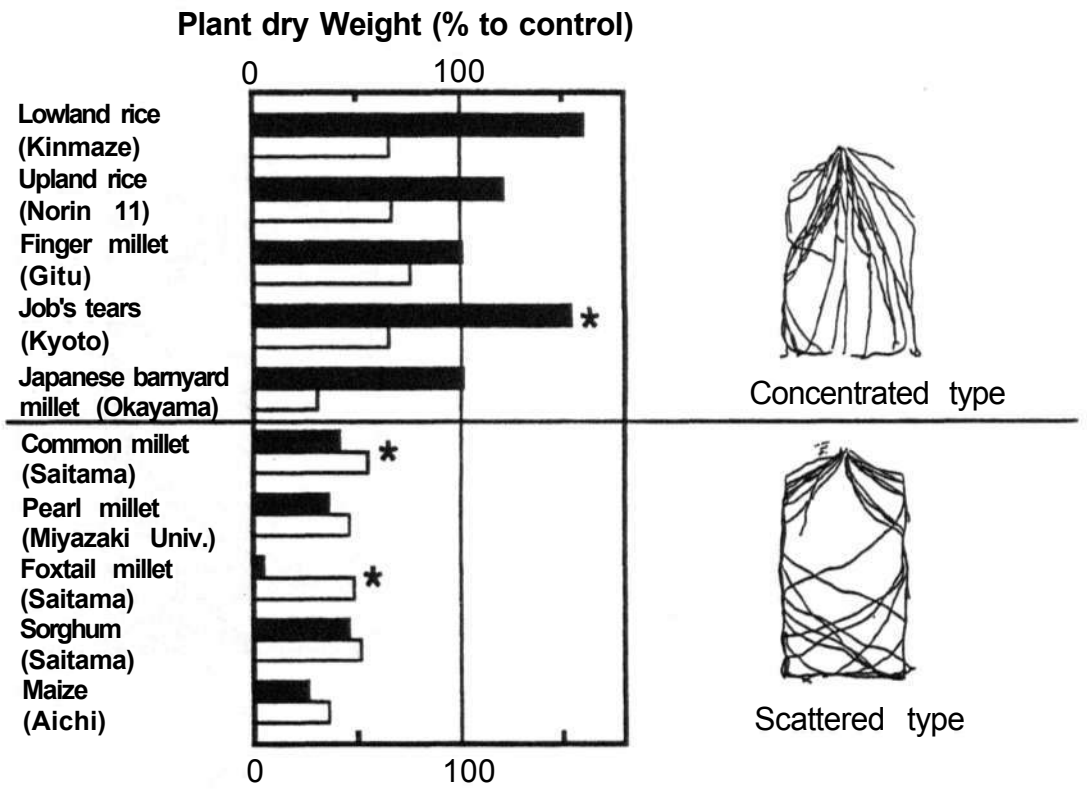


Fig. 4 Dry matter production of 9 species of summer cereals grown under drought (□) and waterlogged (■) conditions until maturity (see details in the text). Values are expressed as a percentage of those of plants grown under moderate soil moisture condition (control)(Kono et al. 1987b). The root system of Job's tears was not classified into the concentrated-type but the structure was similar. Those of common millet and foxtail millet were an intermediate type between the concentrated-type and scattered-type (Yamauchi et al. 1987b).

and water uptake under wet or water-saturated soil where water and nutrient mobility is high. In such wet and oxygen-deficient soil, most of the oxygen required for the physiological functions of the roots is supplied through the cortical aerenchyma from the shoot. The concentrated-type root system that has many short laterals should therefore be more advantageous because the distance to the root tip where the oxygen demand may be highest is relatively short.

To further investigate the mechanism of waterlogging tolerance, the 9 summer cereals were grown under waterlogged conditions, and their growth responses were examined in relation to their ability to produce nodal roots under such conditions (Kono et al. 1988). Results clearly showed that the growth performance of the crop under waterlogged conditions (waterlogging tolerance) was closely related to rooting ability. Detailed growth analysis on rice and maize grown under three different soil moisture conditions from drought to waterlogging was also made (Yamauchi et al. 1988a). This study showed that root growth and function under different soil moisture conditions greatly determined the growth behavior of the plant and reflected their drought and waterlogging tolerances.

We have so far discussed the significance of the root system structure mainly in relation to water and nutrient acquisition. However, our knowledge on root function has increased to understand, for example, that (a) the crop lodging resistance is closely related to the root system development, (b) roots are sites of synthesis of plant hormones and other substances, and (c) roots are also sites of interactions with various microorganisms. For example, Kwak et al. (1996b) found that the rice seminal root axis and its concomitant lateral roots show different changing patterns of endogenous abscisic acid and zeatin riboside concentration with growth. Besides, Yano et al. (1996a) reported that arbuscular mycorrhizas do not distribute evenly in a root system of young peanut seedling, but the first-order lateral roots are the main site for the mycorrhizal development. Furthermore, they indicated that the frequency of the mycorrhizal formation increases acropetally toward the root apex especially in the relatively aged roots that initiated on the proximal portion of taproot axis. These facts strongly suggest that root system structure, which is determined by the development of different component roots, is closely related to those functions but this subject demands further investigation.

Effects of soil stress factors on root system structure and development

Under field conditions, crop growth and yield are usually substantially lower than what is to be expected given adequate solar radiation, air temperature, and genetic potential. This fact is mainly due to environmental stresses, most of which are related to soil factors.

The soil stress factors include chemical, physical, and biological factors. One of the major chemical factors is pH (Foy 1992). In addition to the direct effect of low soil pH, the major problems are the toxicity of soluble aluminum ions and deficiency of phosphorus associated with soil acidification. In contrast, when the soil pH is high, there are alkalinity-salinity problems, which have been extensively studied in relation to dryland farming and desertification (Poljakoff-Mayber and Lerner 1994). On the other hand, examples of the

physical factors are soil moisture, soil air (gaseous composition) (Zobel 1992; Jackson 1985), soil temperature, and soil strength. The biological factors include soil microorganisms, which are also known to affect root system morphology and function (Curl and Truelove 1986; Peterson 1992; Atkinson et al. 1994; Yano et al. 1996b).

Most published research has focused only on any one of the above-mentioned stress factors and evaluated its effects. However, the situation is much more complicated in the field, where these factors interact. For example, the water, air, and strength of a soil are closely related and change simultaneously. Therefore, care needs to be taken in the interpretation of experimental results.

Considering the large amount of research related to soil stress, less has been done on the effects of such stress on the development of plant roots that are directly exposed to stress. It is understood that most cultural practices are targeted at reducing stress factors; hence, root responses should be a key research subject in order to improve crop production systems and technology.

In this section, we will refer to some of our research on the effects of soil stress factors, such as drought, waterlogging, high soil temperature, allelopathic substances, and nitrogen on root system development and structure. In the different studies, special attention has been given to show how different component roots respond to these stresses in different ways, in order to ensure the survival and growth of plants under a particular stress condition.

Soil moisture

Among the various soil stress factors, the soil moisture effect is probably most commonly recognized. Figure 5 shows the root system of rice and pearl millet grown under moderate soil moisture, drought and waterlogged conditions for 1 month. Rice is relatively waterlogging tolerant, whereas pearl millet is relatively drought tolerant. Root system development of pearl millet was drastically affected by the soil moisture condition. Under drought condition the concentration of lateral root development shifted to the deeper soil layers, whereas under waterlogged conditions root development was almost restricted to upper soil layers. These facts indicate that the root system structure can be substantially modified by soil moisture condition and the extent of modification differs with species.

Water shortage

The condition of limited water supply in the soil to support plant growth is the most common form of stress that plants face. Droughted plants generally exhibit a small root system configuration and the reduction in root system size is directly proportional to the magnitude of water shortage in many cases. In cereals, for example, under severe water stress there is a much slower rate of root elongation than under well-watered conditions (Pardales and Kono 1990; Sharp et al. 1988). Fraser et al. (1990) showed that the decreased root elongation that takes place under drought is due to the significant reduction in the rate of cell supply to the cortical layers a few millimeters behind the root apex. This information corroborates the earlier point raised by some researchers (e.g., Molyneux and Davies 1983), that cell growth is the primary process affected by limited soil moisture supply.

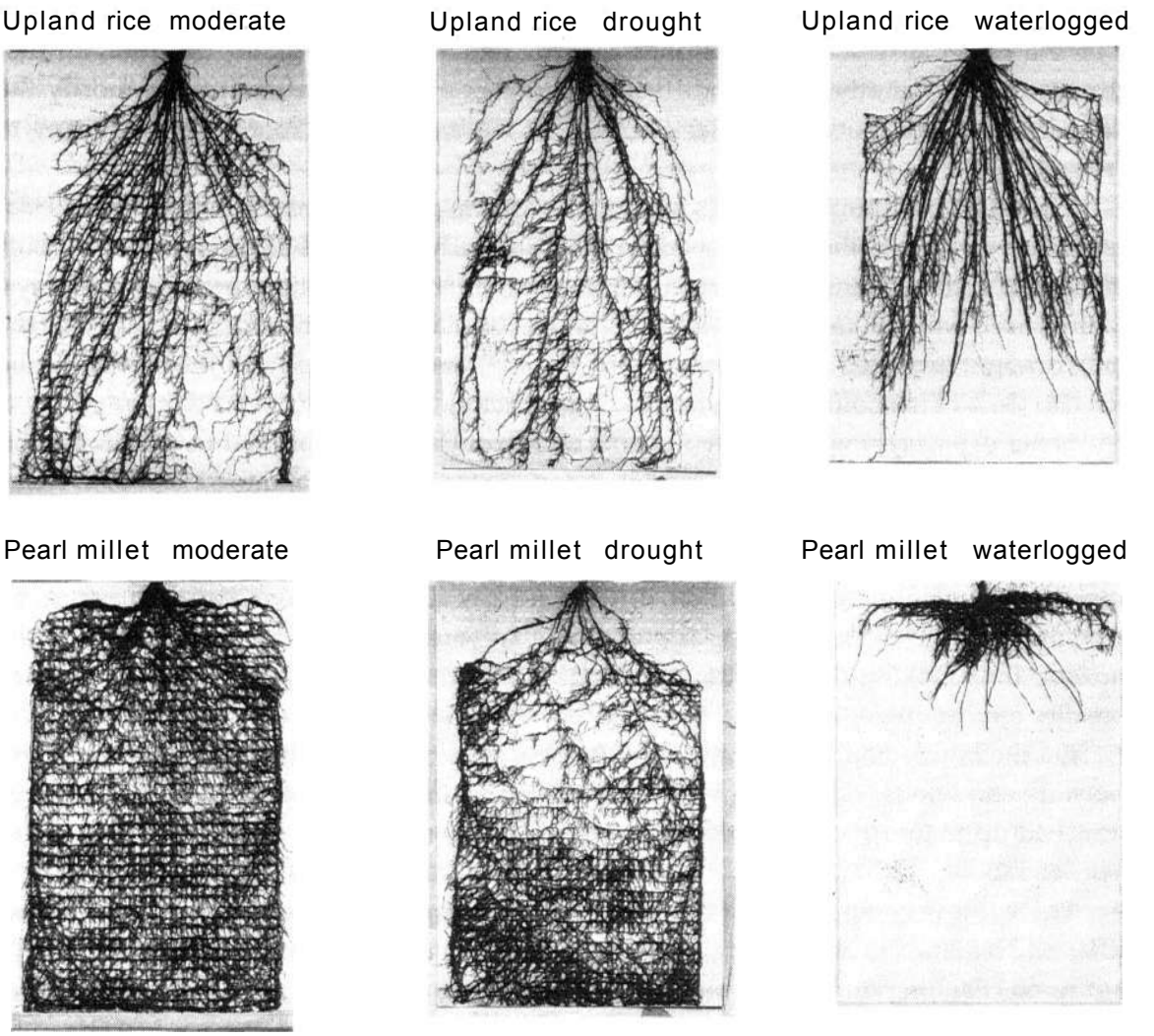


Fig. 5. Root systems of 1-month-old upland rice (top three) and pearl millet (bottom three) grown under moderate (left), drought (center), and waterlogged (right) conditions sampled with the root-box pin-board method. Depth of the root boxes was 40 cm.

However, as stated earlier, soil water stress does not exist in isolation, but is mutually interactive with soil air and strength, all of which integratedly affect the root growth. Previous studies have rarely paid attention to this fact. This is because it is extremely difficult to experimentally evaluate the effects of each factor separately as well as their integrated impact (Taylor and Gardner 1963; Taylor and Ratcliff 1969). Furthermore, Kramer (1983) stated that there have been very few studies that quantitatively evaluate soil moisture stress effects on root growth. This is mainly attributed to the unavailability of experimental techniques to precisely and simultaneously determine the elongation of roots and the water status of the soil.

Consequently, we can find research reports that show conflicting results, i.e., promoting and inhibiting effects of soil water stress on root growth, Taylor (1983) indicated that a soil moisture content of less than -1 MPa apparently retards root growth, whereas in

wetter soil this effect is unclear. On the other hand, mild water stress does not affect root growth (Mia et al. 1996b), or often increases the root/shoot (R/S) ratio, or promotes root growth itself (Weerathaworn et al. 1992). Main concerns of these studies are mostly the elongation of axile roots or root weight, but not the responses of root system structure to dry soil.

The effect of drought on the soybean root system was studied by Kono et al. (1987a) using the root-box method mentioned earlier. This study examined all the component roots in the root system. Plants were grown under three different irrigation regimes for 38 days: control, well-watered (approximately 43% to the maximum water-holding capacity of the soil); drought, irrigated from the top of the box (TI), and irrigated from the bottom of the box (BI) (36% of maximum soil water-holding capacity).

Shoot dry weight was inhibited to 60% of the control in TI plots and to 45% in BI plot, whereas inhibition of root growth was much less, i.e., to 96%) in TI and to 82% in BI in terms of length. The drought treatment substantially increased the ratio in number and length of the third and fourth order lateral roots, which compensated for the inhibited growth of the lower order lateral roots. In addition, drought greatly altered the root system structure by promoting the production of long lateral roots that emerged from the basal portion of the taproot, thus making the direction of elongation of these lateral roots more downward (smaller rooting angle).

On the other hand, there were some root parameters that were rarely affected by soil moisture conditions. Examples of these are the branching order of lateral roots (the plants branched up to fourth order in the three plots) and the ratio of the number of L-type to S-type laterals.

The various components of the root system in some annual plants appear to have different responses to an on-going drought. In the case of sorghum, for example, Pardales and Kono (1990) reported that progressive drought that commenced 12 days after planting first caused a reduction in the number of lateral roots coming from the seminal root and nodal root axes, including the laterals on them. Increasing drought intensity eventually caused complete arrest in the growth of seminal root laterals while new nodal roots and first-order laterals continued to be formed although at a much depressed rate compared with that observed in well-watered plants.

Pardales and Kono (1990) also noted continued root growth in sorghum in terms of number and length of nodal roots under increasing drought intensity. This observation, and the report of Jupp and Newman (1987) that different parts of the root system of *Lolium perenne* tend to have different critical periods at which they succumb to the desiccation effect of drought, suggest that the different root system components in annuals may have different threshold levels at which they succumb to drought.

On the other hand, it may be that a certain level of drought intensity causes promotion of growth in some root system components. For cassava, Pardales observed that a short duration of drought (35 days) either early or late in the establishment phase of the plant (first 90 days from planting) resulted in a greater number of adventitious roots, and thus longer total root length, than in those plants that were well-watered. However, the number of the first- and second-order laterals in early or late droughted plants did not differ from those in the control plants. Substantially lower numbers of lateral roots were observed from

continuously droughted plants.

The increase in root growth under a given drought intensity is not well understood and thus needs to be clearly established because of the seemingly beneficial implication it will contribute to the general performance of plants growing under water stress conditions. The changes in the amount of available water with regard to soil layer is known; however, the cause of differentiation in root system components' distribution in the soil needs to be further investigated. Osonubi and Davies (1981) and Kono et al. (1987a) mentioned that a water deficit in the upper soil layers promote deeper root penetration, thereby allowing the plant to effectively use the available water stored deeper in the soil profile.

O'Toole and Bland (1987) extensively reviewed the literature on plant root system morphology and discussed their phenotypic plasticity. We believe that it is only by examining the development of each component root that we can distinguish "plastic" and "conservative" traits and understand how the root system responds to drought as an integrated system.

Excessive moisture

Excess water in the soil, or waterlogging, caused by flooding or merely saturation of the soil for longer periods, brings about alterations in the development of the root system in strictly terrestrial plants, and most of these alterations are adaptive in nature. The first effect of excessive water when this occurs during the growth of a plant is a change in the general root system morphology, apparently caused by the significant decrease in gas exchange between the atmosphere and the soil (Kozlowski 1984). Under waterlogged conditions, the plant roots have to function in anaerobic soil, and there are at least two morphological adaptations that roots exhibit in response to anaerobisis, i.e., development of new adventitious roots (Kono et al. 1988; Yamauchi et al. 1988b) and superficial rooting (i.e., the concentration of new root growth in the upper layers of the soil) (Jackson and Drew 1984).

In a study to determine the dynamics of root system development under waterlogged conditions, Pardales et al. (1991a), working on sorghum, found that progressive waterlogging markedly restricted the elongation of the nodal or adventitious roots, the seminal root, and the lateral roots. Nodal root production (increase in number) continued to take place, however, in the sense that when adventitious roots in the lower nodal position of the plant's stem die due to waterlogging injury, new adventitious roots appear at the next highest nodal position. There appears to be a direct relationship between the death of older adventitious roots and the development of new ones. Progressively waterlogged plants generally show smaller root system size than those grown in a well-drained condition.

Sorghum plants that were exposed to waterlogged conditions for a short period (12 days) early or late in their vegetative growth showed root growth resumption after the waterlogging was relieved (Pardales et al. 1991a). Regrowth was mostly through re-elongation of existing functional adventitious root axes and lateral roots and initiation of new laterals in the early waterlogged plants, whereas in the late-waterlogged plants it was related more to the development of new adventitious roots.

High temperature

Another major stress factor that influences the root growth of many crops in the tropics and subtropics is high root zone temperature (RZT). For many crops, 25-30 °C is the optimum RZT for normal root development (Nielsen 1974). Departures from this range commonly cause inhibited root growth and development (Abbas Al-ani and Hay 1983; Barlow and Adam 1989; Pardales et al. 1982; Walker 1970). Root characters that are strongly affected by RTZ include root diameter, rooting depth, and rooting angle (Rendig and Taylor 1989).

In trying to determine the response of the different root system components of sorghum to hot thermal regimes in the root zone, Pardales et al (1991b) worked on hydroponically cultured plants exposed to normal (25 °C), high (40 °C), and alternating high and normal (40 °C/25 °C day/night temperatures) RZTs. A suppressed seminal root growth was observed from the constant high RZT and the alternating high/normal RZT, but suppression was more severe at the constant high temperature. The number of first-order lateral roots and their elongation rate were also reduced markedly by the same temperature. Root growth in terms of seminal root elongation, first-order lateral root number, and their elongation, was found optimum under normal RZT,

The exposure of the root system to different periods of high RZT greatly affects the subsequent development of the same roots under normal RZT. The longer the exposure to 40 °C, the shorter the length of the seminal root axis and the fewer the number and the shorter the length of the lateral roots on it. On the other hand, the nodal or adventitious root development tends to be enhanced by exposure time (2-6 days) to 40 °C. This result suggests that, as in the drought and waterlogged conditions, the promotion of nodal root development is an adaptive response of sorghum to high RZT stress.

The suppressed growth of high temperature stressed roots is due to the shortening of the cells in the cell layer behind the root apex (Pardales et al. 1992a). The degree of inhibition of cell elongation increased with the increase in exposure time to high RZT. The cell production rate is similarly affected by high RZT.

Allelopathic substances

The evidence for allelopathy has accumulated over the years and it has been shown that sensitive plants succumb to allelopathy in a number of ways, i.e., either reduced germination, lack of seedling vigor, plant death, leaf yellowing, or stunted and deformed roots or tops (Lovett and Ryuntyu 1992; McCalla and Haskins 1964; Rice 1974). Although the roots are the primary organs of the plant that come into direct contact with the allelopathic substances in the soil, there is no clear understanding on how they respond to allelopathic stress. Relatively recently, however, Pardales and his co-workers (1992b) reported that allelopathic substances from taro *(Colocasia esculenta)* residues significantly reduce the root growth of sorghum. Based on the control, the seminal root elongation was suppressed by 12%, whereas that of the first-order laterals was inhibited by 37%. The number of the first- and second-order laterals was also limited by as much as 46% and 67%, respectively. Development of new first-order lateral roots and their elongation was

arrested on the side of the seminal root that contained allelopathic substances (Fig. 6). Generally, these facts show that allelopathic stress modifies the root system morphology of allelopathy-sensitive plants by inhibiting growth of all the components of the root system.

Pardales (1993) similarly found root growth reduction in sweet potato plants grown in soils previously planted with sweet potato *(autoallelopathy).* Reduction in growth of sweet potato roots was basically attributable to reduced number and elongation of the different root system components, including the adventitious roots. It is highly possible that allelopathic substances interfere with the meristematic processes in the roots resulting in an impaired cell division, or that they inhibit cell elongation or hormone-controlled root initiation (Charlton 1991).

Nitrogen availability

One of the important characteristics for high-yielding modern crop varieties is adaptability to heavy manuring (AHM), especially of nitrogen (N)-containing fertilizers. Although many studies have been conducted on N-uptake, metabolism, its roles and functions in plant growth, etc., the effects of N on root system development are not well understood. Nitrogen is required to achieve high yield, but for good root growth N sometimes acts as a stress factor. Kawata et al. (1977) reported that heavy application of fertilizer-N in paddy fields inhibited the root growth of rice, especially root elongation, which resulted in the formation of a smaller-sized root system.

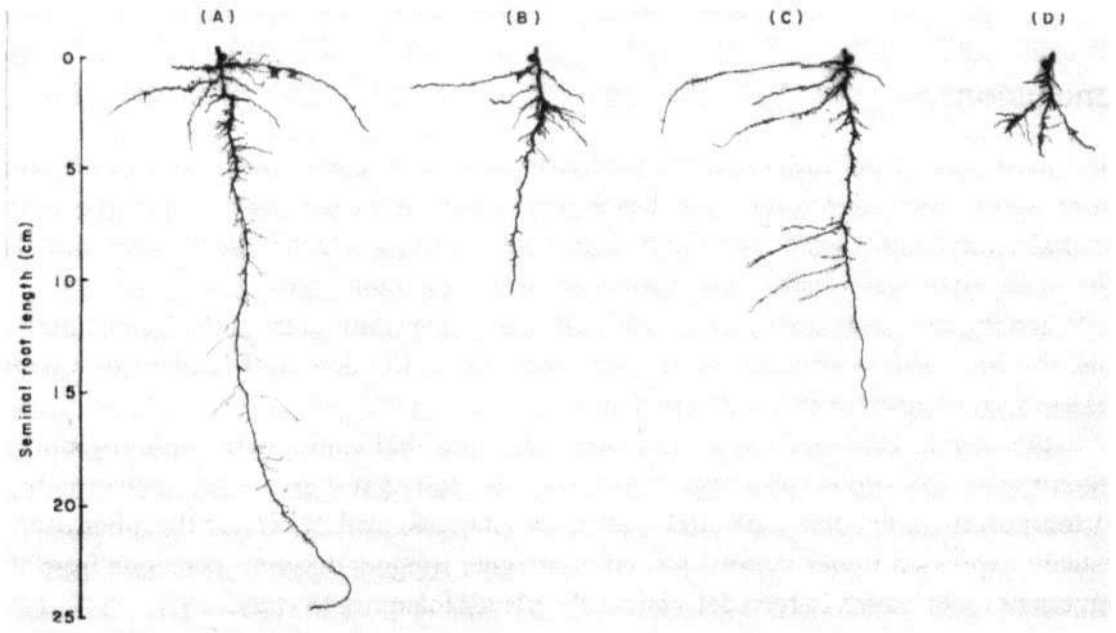


Fig. 6. Development of seminal root system affected by taro residue incorporated into a sand growing-medium. Plants were grown in root boxes for 15 days, and the root systems were sampled and photographed using the root-box pin-board method. (A) no residues incorporated; (B) residues incorporated in the whole sand profile; (C) residues incorporated into one-half (right) of the sand profile; (D) residues incorporated into the uppermost 2 cm (Pardales et al. 1992 a).

In these respects, we conducted a series of experiments to examine the effects of N (especially ammonium-N) on the development of the components of the rice root system, and the general root system structure. The seminal root elongation of several rice cultivars was investigated under different ammonium-N concentrations in solution culture (Tanaka et al. 1993a). The effect was inhibitory and started even at a very low (0.4 mg L^{-1}) N-concentration. Besides, there were clear cultivar differences and those with high AHM were less affected in terms of the seminal root elongation than those with low adaptability.

Another experiment was conducted to examine the whole root system response at different growth stages to different N-application regimes in the soil culture (Tanaka et al. 1993b). As the amount of N-application increased, there was a tendency for the plant to produce more roots but their elongation was inhibited. The cultivar with low AHM formed a longer root system by producing more nodal roots whose elongation was only slightly inhibited as the amount of N applied was increased. This slight inhibition of nodal root elongation by high levels of N-application appears to be associated with the increased production of lateral roots, especially thin roots. In contrast, the root system development of cultivars with high AHM remained relatively unchanged by the N-application regime, except for the nodal root production that was enhanced. In addition, Tanaka et al. (1995) compared the root response to different N-application regimes among four rice cultivars with different AHM, and found that the phenotypic plasticity in root system structure is particularly large in a cultivar with low AHM. These facts indicate that the response to N in the growth medium differs among component roots and plant growth stages, which at least partially determines the AHM of the rice cultivars.

Conclusion

The root system of an individual plant consists of several component roots of different nature. Recent research has revealed that these component roots differ not only in external morphology and ontogeny but also in their internal anatomy, which indicates that they also differ in physiological functions and genetic control of their initiation.

When the root system structure is defined as an integration of the different component roots, the root system structure is of great significance in allowing the plant to tolerate stresses, such as drought and excess moisture.

Experimental evidence has accumulated showing that component roots respond in different ways to various soil stress factors, such as limited and excess soil moisture, high soil temperature, existence of allelopathic substances, and N. Thus, the phenotypic plasticity expressed under various soil environments triggers different reactions from the component roots, which in turn determines the plant's tolerance to stress.

Acknowledgment

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Genotypic Variation in Root System Development and Its Implications for Drought Resistance in Chickpea

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Abstract

Root mass and the developmental pattern of the root system of chickpea play a significant role in yield determination when chickpea is grown in residual soil moisture under rainfed environments. Despite such importance, studies on root growth and its genotypic variability are scanty for chickpea. There is a need to identify and exploit the genetic variability in root traits for better adaptation to water-limited environments. This paper assembles recent information on root growth dynamics in chickpea.

In terms of total root length and root biomass, root growth pattern is sigmoidal with the rapid growth phase continuing up to the mid-podfill stage. Chickpea is one of the deepest rooting species among the cool season food legumes. The average rate of root penetration of field-grown plants was about 20 mm day^{-1} in spring, and was as slow as 5 mm day^{-1} in winter months at International Center for Agricultural Research in the Dry Areas (ICARDA), Syria. The rooting depth is normally about 1.20-135 m with large environmental variations. Genotypic variation according to rooting depth is available. The lateral spread of roots is adequate and early enough to exploit the inter-row space. The ratio of root to total plant for chickpea is much smaller than that in cereals and continues to decrease with the age of the plant. A recent study at ICRISAT Asia Center using sand-culture grown plants revealed a large genotypic variation at the seedling stage for this trait. Such variation permits a rapid, less-expensive screening method. Under receding soil water situations, fine roots at the surface soil died while root growth continued at deeper layers. There was a large genotypic variation in the extent of root proliferation, reflecting the soil water depletion. A deep root system seems to be related to yield under drought stress and drought tolerance. The root system in chickpea is likely to be sub-optimal at depths below 75 cm because large amounts of water were left unextracted at maturity. Furthermore, there was a positive, linear relationship between root length density and the amount of water extracted at the active water extraction front.

An early-developed prolific root system with a vigorous shoot growth maximizes transpiration over evaporation of surface soil water. Therefore, chickpea improvement efforts for water-limited environments should incorporate early root and shoot growth vigor for better adaptation. While adequate information on growth and timing of root system development in chickpea is available, little

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is known about the extent of genotypic variation for various root growth characteristics. To identify contrasting sources of variation, sand culture has been proposed as the most suitable medium.

Introduction

Improvement in crop root systems has lagged behind that in above-ground plant characteristics (OToole and Bland 1987) despite the vital role of these characteristics in the supply of water and nutrients to the entire plant. This disparity can be attributed to the root system's concealment in the soil and variable nature, both of which enormously complicate observation and experimentation (OToole and Bland 1987). The importance of studying plant root systems has increased with increasing interest in aspects such as root biosynthesis of compounds involved in regulating plant development, root exudates influencing absorption of sparingly available P (Ae et al. 1991), interaction of roots with mycorrhizal fungi and symbiotic nitrogen fixation.

Chickpea is one of the most widely grown pulses in the world. This crop is usually grown on residual soil moisture stored during the rainy season and on marginal soils. As a consequence, chickpea is generally exposed to varying degrees of terminal drought stress, as determined by the previous rainfall, atmospheric evaporative demand, and soil characteristics, such as type, depth, structure, and texture. Although in several regions, irrigation has lead to the realization of economically competitive and more assured grain yields with the use of improved disease-tolerant genotypes as in peninsular India (Saxena 1984) and the spring-sown crops in Syria (Silim and Saxena 1993a, b), a major proportion of the world's future chickpea production is likely to continue to come from rainfed agriculture. One avenue for crop improvement in these diverse rainfed agricultural complexes lies in optimizing root systems to minimize soil-related stresses. Success in this endeavor depends on our ability to define and understand the edaphic environment while exploiting the range of genetically based adaptability in a crop species (OToole and Bland 1987).

Despite the economic importance of chickpea and the necessity for it to survive and produce on water stored in the soil, relatively little attention has been given to the root systems and their role in influencing the pattern of water use. Genetic improvement of crop species requires knowledge of intraspecies variability in appropriate root parameters and the genetic control of this variability. Such useful variability has been reported, and indeed used, for crop improvement with variable success in several crops, such as in wheat (Hurd et al. 1972a, b and 1973).

In this brief review, we attempt to assemble relevant descriptions of root growth dynamics and genotypic variation in morphological characteristics related to the spatial and temporal expansion of the root system of a growing chickpea plant. The implications of such genotypic differences in root systems in relation to improvement of chickpea adaptation to drought are emphasized. Major data requirements for this review has been drawn from a recent root study carried out at ICRISAT Asia Center (IAC).

Methods of root study

Field measurement

Identification of genotypic variation in root growth depends on the use of a reliable and reproducible screening method. Screening for most shoot parameters in field conditions is easily possible, whereas for root parameters it is complicated and difficult due to the root system's concealment and associated soil variations.

In most of the chickpea root studies involving in situ observations reported in the following pages, the auger method was used. This method provides for a three-dimensional volumetric measure of soil-root relationships and permits use of larger machine-driven augers. In a majority of the reported work, results of which are reviewed here, this method was adopted (Sheldrake and Saxena 1979; Silim and Saxena 1993a; Siddique and Sedgley 1987). A recent field study conducted in a Vertisol at IAC involved sampling by a monolith method. Monoliths of soil were cut from an area of 20 x 30 cm to a depth of 10 or 15 cm successively and removed from an access pit. The roots from the extracted soil mass were washed in a 1.0-mm sieve after soaking the soil overnight. Advantages of this method over the auger method include the reduction in the extent of sampling variation and the early assessment of causes leading to abnormalities. However, both of the above-mentioned field methods are suitable only for limited comparisons. When the comparisons are many, i.e., involving a large number of genotypes or treatments, the use of rhizotron/minirhizotron methods can be appropriate. However, none of the chickpea work reviewed here applied the rhizotron/minirhizotron method for root studies. This method provides a unique opportunity to study plant root systems continuously in situ. The modern video minirhizotron system provides not only information on rooting depth and density in field situations, but also estimates of changes in root orientation and morphological characteristics with less limitation on the number of observations. However, this method also has its limitations. The major drawback is that the root density estimates recorded by this method do not compare well with the monolith or auger method estimates.

Screening

Some of the screening efforts reported here used container methods involving solutions or sand or soil as the culture medium. The solution culture methods were successfully adopted for identifying genotypic variation in the rate of extension of the primary axis (Vincent and Gregory 1986) and in root mass (ICRISAT 1988). As the morphology and branching pattern of roots grown in solution culture are very different from those observed in the field, due to unimpeded growth, the scope of this method for screening or evaluation in breeding programs seems to be limited.

The sand culture medium supplemented with nutrients in the form of a nutrient solution has been extensively used at ICRISAT for identifying genotypic difference in root mass. This method was found to be particularly useful in extracting chickpea roots

completely intact and to transplant the plants to an alternate medium or to the field for regeneration after recording the root volume (ICRISAT 1988; ICRISAT 1989). Use of this method lead to the identification of contrasting rooting characteristics among chickpea genotypes, including Annigeri and ICC 4958, and, later, some single plant progenies with large root mass. Although the sand culture medium was also an artificial environment, with the risk of limited applicability to field situations, later studies showed that the genotypic differences thus obtained were reproducible in the field (ICRISAT 1994).

Root system development

Root type

As in many of the dicotyledons, the radicle of a chickpea seedling grows into a well-defined tap root system. Normally, the tap root branches into laterals at the time of seedling emergence, i.e., within 6 days after sowing both in field and greenhouse grown plants (Fig 1). The lateral roots may themselves branch (second-order laterals), but it is unusual for further orders of branching to occur in the field (Gregory 1988). With a replenishment of surface soil water by irrigation or rain, the underground portion of the stem is capable of producing adventitious roots, even at later stages, such as at podfill, but these roots do not grow as deep as either the tap root or the primary or secondary laterals. It is likely that this adaptive mechanism enables the plants to extract nutrients and water from surface soil layers whenever such an opportunity of surface water availability occurs.

The tap root growth is strongly geotropic, whereas the laterals emerge at angles of about 45° to the tap root and grow for some distance before turning downwards (Fig. 2). Generally, the tap root of *desi* chickpeas with a spreading-type shoot growth habit loses its apical dominance between 10 and 20 cm of length whereas the tap root of most of the kabulis and tall-types continues to grow deep.

Temporal changes in root growth

Figure 3 shows the overall pattern of root growth for two chickpea genotypes grown in a Vertisol soil in 1992/93 and 1993/94 postrainy seasons at IAC with progressively receding soil water. In these studies, roots were collected by the soil-root monolith sampling method from an area of 20 x 30 cm to 135 cm depth with intervals of 10 or 15 cm. Samples were collected at about fortnightly intervals, and root length was measured using a root length scanner (Comair, Commonwealth Aircraft Corporation Limited, Australia). The growth pattern in terms of root dry matter accumulation and total root length was approximately sigmoidal. In both genotypes, root length and dry matter increased rapidly until about the mid-podfill stage, after which the growth was much slower. A similar pattern of temporal growth was observed for both winter- and spring-sown crops of chickpea variety ILC 482 in northern Syria (Gregory 1988) and of three varieties including ILC 482 (Brown et al. 1989) and of varieties JG 62 and T 3 at Hyderabad, India (Sheldrake and Saxena 1979). Genotypic

Fig. 1. Genotypic variation in root and shoot growth in chickpea. Seedlings were harvested from sand culture 6 days after sowing at the ICRISAT Asia Center. Genotypes from left: ICCC 42, ICC 4958, Annigeri, and ICCV 90039. Note the restricted shoot growth in ICCC 42, whereas the lateral root growth is fairly vigorous.

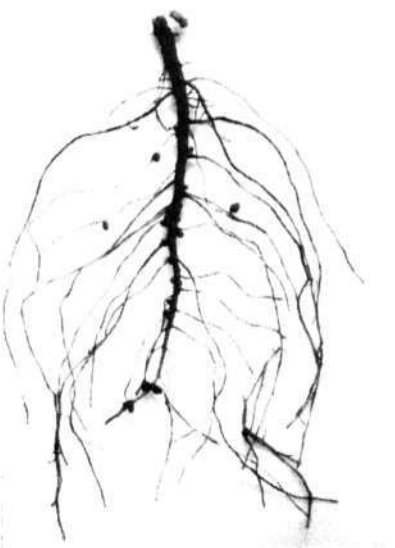

Fig. 2. Branching pattern of a root in chickpea. Roots of a field-grown plant at 37 days of age, extracted to a depth of about 20 cm, Vertisol, ICRISAT Asia Center.

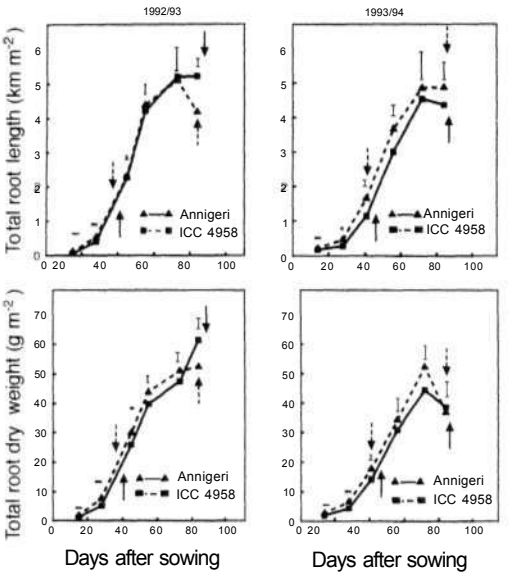

Fig. 3. Seasonal changes in root growth of two chickpea genotypes grown in a deep Vertisol under progressively receding soil moisture conditions during the 1992/93 and 1993/94 postrainy seasons at the ICRISAT Asia Center. Arrows indicate time of 50% flowering and maturity. Vertical bars denote SE.

variation was evident for both total root length and root dry matter at the early stages of crop growth, i.e., before 50% flowering. Genotype ICC 4958 produced a relatively longer total root length and higher root dry matter compared with Annigeri during 1993/94. This was also demonstrated earlier using a sand-culture medium in a greenhouse (ICRISAT 1989). However, later growth of Annigeri was able to fully compensate for this difference, at least during the first year.

It is unclear from the available literature as to the stage at which root length ceases to increase or dry matter accumulation stops. The continuation of dry matter accumulation and its rate seems to be influenced by soil water and above-ground environments. Factors that positively influence more partitioning into the vegetative structure (e.g., high soil moisture, short photoperiod, cool temperature) are likely to promote better root growth. Siddique and Sedgley (1987) measured maximum root length at about 30 days before harvest in the *desi* type CPI 56288 at Merredin, Western Australia. These results suggest that, as with cereal crops (Gregory et al. 1978, 1984; Siddique et al. 1990), most root growth of chickpea occurs before the onset of reproductive development. These results can be considered unique due to the exceptionally long vegetative phase (about 90 days) in an environment supporting a short growth duration (about 120 days). Therefore, we conclude that due to the indeterminate nature of chickpea, root growth is possible even during the reproductive stage, although this is largely determined by environmental conditions. Influence of growth habit on continued root growth has been well demonstrated in soybean. Substantial root growth has been shown to occur at depth after podfilling in the indeterminate varieties, whereas no further growth occurs in the determinate varieties (Kaspar et al. 1978). In perennial crops like pigeonpea, the roots continue to accumulate dry

matter and produce laterals throughout the growth of the plant until it is harvested (Chauhan 1993). Under more temperate environments in the UK, although the total length of the faba bean root systems increased until close to maturity in Wellesbourne, Warwick (Greenwood et al. 1982) the gain in root dry weight in another location, some 80 km distant, ceased about 60 days before maturity (Hebblethwaite 1982).

The average rate of chickpea root growth in Vertisols at ICRISAT Asia Center was about 20 mm day^{-1}, which is more like a spring-sown crop at ICARDA, Syria (Brown et al. 1989), reaching 1.20 to 1.35 m of soil depth by about 72 days from sowing (Fig. 4). During the winter at ICARDA Center in Syria, roots penetrated at about 5 mm day^{-1}, but this increased to about 20 mm day^{-1} during March, a rate that was consistently achieved by all spring-sown crops (Brown et al. 1989).

Rooting depth

In deep Vertisols at IAC, chickpea roots grow to a maximum depth of 1.20-1.35 m (Fig. 4; Sheldrake and Saxena 1979). Roots of common beans seem to penetrate deeper in response to constantly depleting soil water at the surface soil layers (Sponchiado et al. 1989). In a comparison under well-irrigated situations in a sandy loam soil at Hisar, India, Bhatia et al. (1977) found that the chickpea roots were able to grow to a maximum depth of 1.2 m, whereas wheat roots could grow to a depth of 0.9 m. They also found that the roots grew deeper with increased soil moisture at the time of sowing. Available information on maximum rooting depth varies to a large extent. At Coimbatore, India - a warm

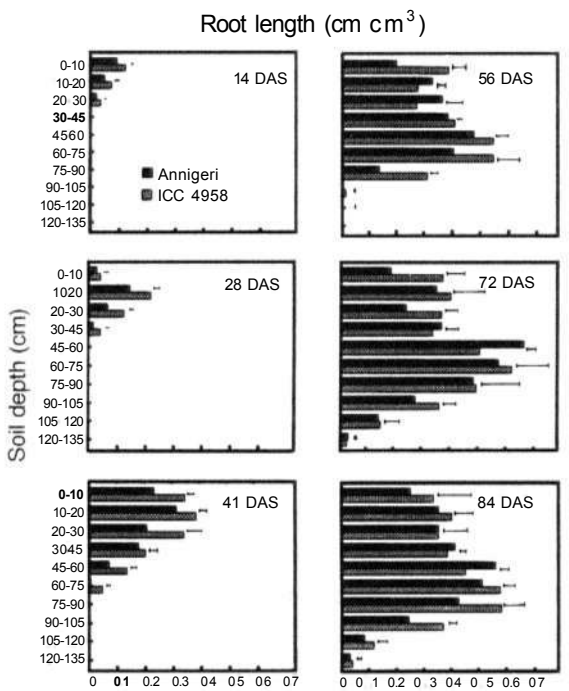

Fig. 4. Genotypic differences in root length distribution over soil depth and time under progressively receding soil moisture conditions in a Vertisol during the 1993/94 postrainy season. Horizontal bars denote SE for comparison of genotypes within a depth.

environment with a short and mild winter providing for a short growing duration - variety CO 1 was found to develop roots to a depth of 0.28 m (Subramanian et al. 1980), whereas in an environment providing for a long-duration (164-169 days), chickpea grown in a sandy loam soil at Ludhiana, India, the roots were observed to grow as deep as 2.7 m (Aujla and Cheema 1985). In other crop species, such as common beans (Sponchiado et al. 1989) and soybean (Kaspar et al. 1978), information on genotypic differences in rooting depth is available. Such information is relatively scarce for chickpea. Though differences in root length density between two drought-resistant genotypes of chickpea, i.e., Annigeri and ICC 4958, in any discrete soil layer is evident, there is no marked difference for rooting depth (Fig. 4). If the extent of variation in shoot canopy architecture and growth duration are any indication, it is likely that such variation in root growth pattern is also available. Silim and Saxena (1993a) found that the effective rooting depth (the maximum depth of water extraction) by spring-sown chickpeas varies from 0.75 to 1.50 m. These depths represent the probable depths of root penetration. Large varietal variation was demonstrated in effective rooting depth among four desi chickpea varieties in an alluvial sandy loam under nonirrigated conditions (Nagarajrao et al. 1980). Variety BG 203 was found to be the best in extracting water at depth (120 cm) and also in having a prolific root system.

Spatial distribution

Figure 4 shows the changes in root length density over depth and time for two chickpea genotypes grown in the 1993/94 postrainy season in a Vertisol soil at IAC. The extent of the root system increased with the age of the plants. Root length density approached a maximum level in the upper 30-cm soil layer at about the time of 50% flowering (41 days after sowing). At this stage, about 66% of the total root length and 82% of the total root plus nodule dry weight of Annigeri was found in this layer. Corresponding values for ICC 4958 were 65 and 77%. Maximum root formation occurred at 72 days after sowing, or 12-15 days before maturity. At this stage, more than 95% of the total root length and total root weight was confined to a depth of 0 to 105 cm. Up to 5 km of total root length could be found below each square meter of soil surface, with root length distribution varying from 0.03 to 1.00 km m^{-2} at different depths.

A reliable prediction of root length distribution in the soil profile gains importance when considering the difficulties and variations involved in root extraction. Several studies (e.g., Greenwood et al. 1982) have successfully used the following expression to approximate the distribution of root length in the soil profile:

$$L_v = L_{v0} \exp(-qz) \quad (1)$$

where L_v is the root length density, L_{v0} is the root length density at time t and depth z = 0, and q is a constant that varies with time. The assumption was that in a uniform soil, root distribution decreased exponentially with soil depth and the rate of decrease (q) decreased with the age of the plants. Equation 1 has been applied to chickpea (Brown et al. 1989; Gregory et al. 1994 to the data of Siddique and Sedgley 1987). This equation was able to reasonably describe the root distribution of both winter- and spring-sown chickpea at

ICARDA with a characteristic age-related reduction in q values (Brown et al. 1989). In chickpea grown at Merredin in Western Australia, although approximation to this equation was possible, the q values did not show a decrease with age. The data set shown in Figure 4 failed to show an exponential pattern at crop growth stages after flowering.

A substantial turnover of roots, particularly in the upper soil layers, is evident in chickpea. Using the data of Siddique and Sedgley (1987), Gregory et al. (1994) demonstrated that root growth in the upper 20 cm only occurred until flowering (95 days after sowing) and that thereafter there was a substantial decay above 20 cm while root proliferation below 20 cm continued. The data for peninsular India indicated a similar root growth pattern in the top-most layer even before flowering (Fig. 4). Considerable root growth occurred below the 60-cm depth and then ceased above this level from 60 days after sowing.

The lateral spread of chickpea roots seems adequate to exploit soil water and nutrients from a commonly practiced 30 cm row spacing. The study conducted by Subramanian et al. (1980) in which the cut shoot-end of the plants was injected with radioactive P, revealed that about 50% of the roots were present at 15 cm from the plant's base compared with the root length density at 5 cm from the plant's base. In a similar study using ^{32}P on loamy sand soil at Hisar in India, Bhatia et al. (1977) demonstrated the lateral distribution of roots extend beyond 15 cm from the plant's base. This lateral spread was found to increase when soil moisture levels at sowing time were higher.

Root to total plant ratio

The ratio of root to total-plant undergoes a large temporal reduction. Also, large environmental variation is evident for this characteristic. As the age of the plants increases a higher proportion of dry matter is partitioned into the leaves and, later, to the reproductive parts. In a chickpea crop grown in Vertisol under progressively receding soil moisture conditions at IAC, a root:total-plant ratio of 0.32 in Annigeri at the seedling stage (13 days after sowing) gradually reduced to 0.10 at the approach of crop maturity (Table 1). Gregory (1988) showed that root weight of chickpea as a fraction of total plant dry weight decreased from 0.5 during early growth to 0.13 at maturity. Brown et al. (1989) observed a similar pattern of reduction in root:total-plant weight in winter- and spring-sown chickpea. At all comparable growth stages the spring-sown crop was found to maintain a higher ratio over the winter-sown crop.

Large genotypic variation in root:total-plant ratio appears to be available in 6-day old seedlings grown under a sand culture system (Fig. 1 and Table 2). In solution culture, such genotypic differences were also reported to persist in 3-week old chickpea plants (Vincent and Gregory 1986) and at 45 days after sowing (Saxena et al. 1993).

Table 1. Changes in root: total-plant ratio over time of crop growth in two chickpea genotypes grown in a Vertisol under progressively receding soil water conditions at ICRISAT Asia Center, postrainy season 1993/94.

Days after sowing	Root: total-plant ratio		
	Annigeri	ICC 4958	SE(±)
14	0.32	0.31	0.039
28	0.24	0.25	0.032
41	0.25	0.22	0.008
56	0.21	0.17	0.035
72	0.15	0.16	0.021
84	0.10	0.09	0.008

Table 2. Genotypic variation in root: total-plant ratio of chickpea grown in sand culture at 6 days after sowing. Representative plants used for this study are shown in Figure 1.

Genotypes	Root: total-plant ratio
ICCC 42	0.64
ICC 4958	0.51
Annigeri	0.49
ICCV 90039	0.42
S.E(±)	0.015

Root growth and its relationship with soil water extraction

Passioura (1982) estimated that a root length density greater than 0.5 cm cm^{-3} soil can be adequate for complete extraction of available water. The maximum root length density as seen in Figure 4 never exceeded 0.5 cm cm^{-3} at most soil depths, even in the peak root growth phase. Other available information also indicates presence of either less (Brown et al. 1989) or marginally more (Gregory et al. 1994) root length density in chickpea genotypes. The chances of identifying a genotype with a larger root length density than that of ICC 4958 are limited, because this genotype was one of the few selected out of more than 1500 germplasm accessions screened for drought tolerance over time in a semi-arid environment (Saxena et al. 1993). Measurements of rooting depth and root length density need not necessarily give an estimate of the ability of the genotype to extract soil water. Soil water extraction within newly explored rooting zones (where the available soil water is >75% and the root tips are expected to be more abundant) is positively and linearly related with the mean root length density up to a maximum of 0.4 cm cm^{-3} soil (Fig. 5). Thus, it is apparent that the chickpea root system is suboptimal for soil water extraction. The poor branching frequency of chickpea roots when compared with roots of other legumes (Gregory et al. 1994) further limits the number of root tips available for soil water extraction.

Genotypic variation in the extent and timing of water extraction is evident in chickpea. Nagarajrao et al. (1980) demonstrated large varietal differences in the time of water

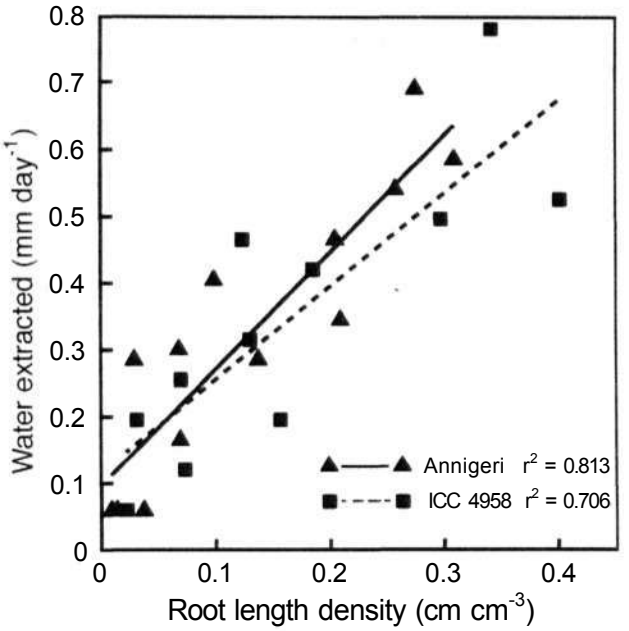

Fig. 5. The relationship between root length density and the rate of water extraction at the active water extraction front (the data points were from depths below 30 cm and from various depths depending on the shift in rooting front).

extraction. Among four chickpea varieties compared in an alluvial sandy loam field under rainfed conditions at New Delhi, India, variety BG 203 was found to deplete the least moisture at 6 weeks after sowing and the most prior to harvest. Moreover, this variety was also able to deplete more moisture at depth. The moisture depletion pattern caused by variety T3 was opposite to that in BG 203. In the recent work at IAC, volumetric water content of the soil under the two genotypes at 50% flowering and at complete maturity is shown in Figure 6. Genotype ICC 4958, with its prolific root system, was able to extract significantly more soil water from surface soil layers (0-30 cm) until about flowering time (Fig. 6). However, these differences in soil water content were not evident at maturity.

Influence of rooting pattern on drought resistance

In water-limited environments there is normally a strong positive linear relationship between water transpired by the crop and biomass formation (Fischer and Turner 1978; Tanner and Sinclair 1983). Therefore, in the present context of this paper, adopting the following expression of Passioura (1977) to describe the differences in yield formation may be more appropriate:

Grain yield = Water transpired x water-use efficiency x harvest index

Differences in rooting patterns change the amount and timing of water availability to the crop. In deep soils with adequately stored soil water, greater depth and extent of water

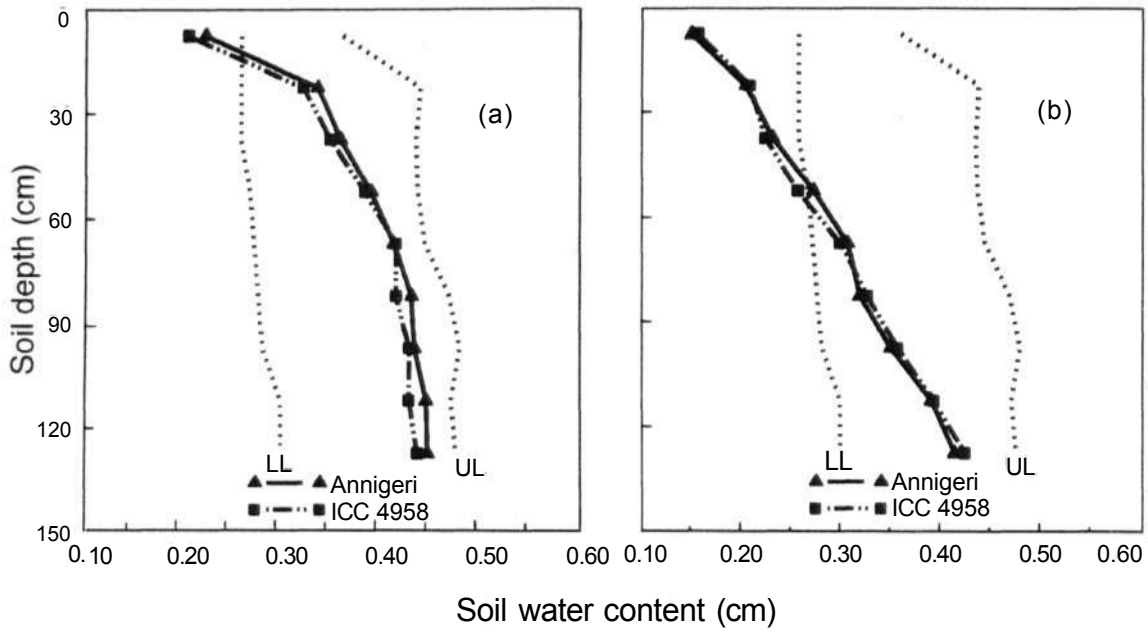

Fig. 6. Distribution of soil water content over soil depths for genotypes Annigeri and ICC 4958 grown in receding soil water conditions (a) at 43 days after sowing (SE for genotypes within a depth is 0.0026 cm and that for depths within a genotype 0.0056 cm) and (b) at 95 days after sowing (SE for genotypes within a depth is 0.0038 cm and that for depths within a genotype 0.0081 cm). Both genotypes were grown in a deep Vertisol at the ICRISAT Asia Center 1993/94 postrainy season. The symbols UL and LL indicate the upper and lower limits of available soil water, respectively.

extraction could increase the amount of water transpired. The timing of this extraction could influence the biomass production or the harvest index or both. Cultivaral variations were demonstrated in effective rooting depth, and its influence on pre-dawn leaf water potential of spring-sown chickpeas at ICARDA, Syria (Silim and Saxena 1993a). The cultivars with a deep root system were shown to produce high grain yields in at least 2 out of 3 years in the drought stress treatment, confirming the view that under the conditions where crops depend on residual soil moisture, deep rooting is advantageous (Lawn 1988; Ludlow and Muchow 1988). The association between deep root system and drought tolerance has also been amply demonstrated in soybeans (Kaspar et al. 1978) and common beans (Sponchiado et al. 1989). Whereas earliness was identified to contribute in a major way to drought escape in chickpea, a deep root system was identified to increase drought tolerance (Silim and Saxena 1993b). The extent of rooting in chickpea at deeper soil layers is indeed inadequate. Although the roots were shown to penetrate as deep as 135 cm in a Vertisol under peninsular Indian environments, the soil water extraction was complete only to a depth of 60 cm. The root length density at deeper layers (60 to 135 cm) ranged from 0.5 to <0.1 cm cm^{-3}, and about 60 mm of water was left unextracted. Thus, the prospects of improving chickpea grain yield in deep Vertisols through an increase in root system size at depth seem to be promising.

Like for other plant characteristics, such as leaf area index or shoot biomass at maturity, there must be an optimum size for root growth of chickpea in order to extract the maximum soil water while maintaining the transpiration efficiency. Passioura (1982, 1983)

has questioned the value of deep roots in wheat, in such instances when the crops extracted all the available water by maturity, on the grounds that the water transpired to produce C for the extra root growth may offset the extra water gained by deep roots. Furthermore, he also observed that the cost of root growth and maintenance represents clear diversion of assimilates, which might have been used for shoot growth, and thus may decrease the transpiration efficiency. This argument is clearly crop-specific and directed to a situation where the efficiency of roots in soil water extraction can be suboptimal due to excessive size of the root system in relation to the amount of water left unextracted. The extent of root system in wheat can easily be visualized with an example of variety Kulin producing a root:total-plant ratio of 0.31 (with a root weight of 295 g m^{-2}) at complete maturity (Siddique et al. 1990) compared with 0.10 in chickpea. The shoot growth and yield of chickpea in the semi-arid tropics and in the Mediterranean region (spring-sown) is limited by progressively diminishing soil water (Silim and Saxena 1993b). As water stored at deeper soil layers is the only available source during the reproductive stage of crop growth, normal grain-filling depends upon a deep root system. The fact that chickpea root length density is much lower than that of 0.5 cm cm^3 at soil depths below 60 cm, the maximum root length density moving with depth at late stages of growth and much of the water being left unextracted below this depth, are clear indications of suboptimal root size in chickpea.

Two contrasting strategies of root system management can be visualized to maximize grain yields under water-limited environments. The first approach can be an early use of stored soil water, ensuring a vigorous early crop growth, and the second approach can be a conservative early use, leaving enough water for later stages in order to ensure a better harvest index. The first approach has been amply demonstrated for ICC 4958, a drought-tolerant genotype, producing a prolific root system at early stages of crop growth (Saxena et al. 1993; ICRISAT 1989; Silim and Saxena 1993a), which is continued through the podfilling stage and as a consequence extracts more soil water also from the surface soil layers (0 to 30 cm). Soil water in this layer, if not used early, is prone to evaporation both under tropical and subtropical environments. Early use of an increased fraction of this water tends to maximize transpiration at the expense of evaporation. The genotype ICC 4958 also produces a higher root length density at deeper soil layers, which is normally expected to enhance the soil water extraction. Such an enhanced extraction did not occur due to limitation in time available for extraction as ICC 4958 matured two days earlier than of Annigeri. The early shoot growth of ICC 4958 is vigorous (20.4 ± 1.53 g m^{-2} vs 14.0 g m^{-2} in Annigeri at 28 days after sowing), matching the root growth and enabling an early ground cover so as to reduce evaporative water loss. Yet another example demonstrating the advantages of early use of water can be cited for barley. Cooper et al. (1987) showed that the vigorous root and shoot growth and greater root length density at depth exhibited by a landrace, resulted in high evapotranspiration rates throughout the crop season. However, this approach has its limitations. The advantages of this approach can only be realized in environments where the soils are adequately deep and the amount of soil water stored is high. The second approach can be maintenance of a low root:total-plant ratio from the early stages of growth so as to achieve a high transpiration efficiency (Passioura 1983). The root growth of genotypes Annigeri and ICCV 90039 is less (Fig. 1) with a low root:total-

plant ratio. Both genotypes were found to yield well both under moderate drought stress and well-irrigated conditions (ICRISAT 1993). In a deep Vertisol with a progressively receding soil water situation, this approach does not favor highest yields under severe drought stress in a semi-arid environment.

Conclusion

Our review of the literature indicates that adequate knowledge exists for the pattern of root growth, the size of the root system of chickpea, and the volume of soil it is capable of exploiting. All of this information has been collected for certain cultivated or newly developed varieties (e.g., Annigeri, ICC 4958 and ILC 482). Much is yet to be known of the timing and the extent of variation available in the vast germplasm collection for these species, to facilitate exploitation of this trait in breeding programs. It is also important that knowledge on root activity and function needs to be improved in relation to rooting depth and density so as to predict the water extraction capabilities of the root system. It is encouraging to note that the performance in rooting potential exhibited in sand culture can be easily repeated in field conditions. This paves the way for the screening of large numbers of germplasm accessions easily, quickly, and less expensively using sand culture methods. This preliminary selection can help in limiting the number of plants manageable for further studies or for selection of parents.

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Root Growth and Soil Water Extraction of Three Pearl Millet Varieties During Different Phenological Stages

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Abstract

Many studies have concluded that soil nutrient supply, especially P, limits pearl millet (Pennisetum glaucum (L.) Br.) production in the Sahel more often than soil water supply. However, P-availability cannot easily be separated from water availability because of its effects upon root and leaf growth, which in turn determine plant supply and demand for water. A 2-year field study in Niger examined the effects of P on three pearl millet varieties' root growth and soil water extraction. By far the greatest root length density (RLD) was in the upper 0.20 m of the soil profile, where growth was greatest between booting and head emergence. The local landrace tended to produce more roots in deeper soil layers, particularly when P was applied. Root growth of the variety ITMV 8001 appeared to respond most strongly to added-P in the surface soil layers. Otherwise, root growth was similar between varieties. In most soil layers, There was a pronounced increase in RLD due to P-application in both years of the study. Relative increases in root counts were greater in deeper soil layers, particularly in 1993. This increase was associated with greater soil water extraction during dry spells, especially from upper soil layers. Little evidence of increased soil water extraction due to added-P could be found during wetter periods, which we attributed to increased soil evaporation caused by lower leaf area in plots receiving no P.

Introduction

Root growth and distribution determine both nutrient and water uptake from the soil profile. Several recent studies in the Sahel have concluded that pearl millet growth is limited more often by soil nutrient availability than by water availability (e.g., Bationo et al. 1989; Payne et al. 1990; Klaij and Vachaud 1992), but the effects of soil nutrient supply and soil water supply upon plant growth cannot be easily separated (Viets 1972). An

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example is that poor pearl millet root growth caused by low soil- nutrient availability results in a smaller soil volume from which to extract water (Cisse and Vachaud 1988; Payne et al. 1990), and increased resistance to water uptake due to the presence of fewer roots (Campbell 1985). Presumably, any genetic variation in rooting habits would causally affect both nutrient and water availability. However, to our knowledge there are no studies from the Sahel that have examined varietal differences in pearl millet rooting habits at different fertilizer rates, or the resulting effects on water use during the growing season.

The objective of this paper is to present preliminary results of a study on root growth and water availability of three pearl millet varieties under different levels of soil P-availability, during two growing seasons of contrasting rainfall distribution.

Experimental

Data were obtained as part of a larger agronomic experiment that compared nine pearl millet varieties grown under three levels of fertilizer application. We measured soil water content and shoot and root growth for three of these varieties at two fertility levels.

The agronomic experiment consisted of a completely randomized block design with four replications. Plot dimensions were 10 x 10.5 m. pearl millet varieties were planted at a spacing of 1.2 m on ridges, with 0.75 m between ridges. For both fertilizer treatments, a total of 30 kg N ha^{-1} was applied as equal splits of urea just after sowing and again at booting. Phosphate was added as 0 or 30 kg P_2O_5 ha^{-1}. Phosphate was broadcast before sowing as single super phosphate.

Shoot and root samples were taken at booting, head emergence, flowering, and maturity for the varieties Sadore Locale (the local landrace), ITMV 800,1 and 1CMV IS 85327. Sadore Locale generally matures in about 110 d, whereas the other varieties mature in about 90 d. On each date of sampling, shoots of two representative pockets were harvested from three plots. Roots were obtained from core samples taken at 0.30 and 0.60 m from the center of the pocket on the ridge and between the ridges. In 1993, additional cores were taken from the center of the pocket. Cores 0.20 m in length were taken with steel tubes of 0.078 m in diameter. Roots were washed from soil cores using a 1- mm sieve. Dead roots were discarded. Root length density (RLD) was determined using the line-intersect method. In 1992, roots from cores of both pockets were washed and counted separately. In 1993, cores from identical depths and sampling positions within the same plot were combined for washing and counting to reduce expense. All root samples were counted on grids of 0.01 m, except for samples taken from the center pocket in 1993, which were counted on grids of 0.02 m.

Soil water content was measured weekly, beginning about 2-weeks after planting, with a field-calibrated neutron probe to a depth of 2.30 m. Water balance calculations were made relative to this first date of measurement, based on the equation

$$ET = dS - (R + D)$$

where ET is cumulative crop and soil evaporation, dS is the change in water stored over the

maximum depth of rooting, R is cumulative rainfall, and D is cumulative drainage from the root zone. The parameter D was calculated using the two-stage method of Klaij and Vachaud (1992). During the second stage, i.e., after the wetting depth passed the deepest depth of the neutron probe measurement, D was calculated as a function of water content using the hydraulic conductivity function published by Klaij and Vachaud (1992).

Rainfall and phenology

In 1992, rainfall before planting (153 DOY) was adequate for germination and early seedling growth, but several dry spells occurred between 160 and 200 DOY (Fig. 1). Between 200 and 240 DOY, rainfall was plentiful, but a short dry spell occurred just before harvest (260 DOY), when plants were senescent. Total rainfall in 1992 was 585 mm. In 1993, fields were not sown until 166 DOY. Two brief dry spells occurred between 200 and 220 DOY, when plants were beginning the booting stage. A third dry spell occurred towards the end of the growing season, during plant senescence and grain filling. Total rainfall in 1993 was 536 mm.

The varieties ITMV 8001 and 1CMV1S 85327 had identical phenologies, but phenologies were affected by P-treatment and year (Table 1). Sadore Locale flowered approximately one week later than these varieties in 1992, and two weeks later in 1993. The later planting date in 1993 reduced the number of days to flowering relative to 1992. Generally, lack of P-fertilizer delayed flowering. Because cereals are considered to be particularly sensitive to drought during flowering, this delay could differentially affect crop exposure to drought. The identical harvest dates for all varieties and P-treatments in 1992, and for both fertility treatments of each variety in 1993, were due more to logistical convenience than phenological equivalence.

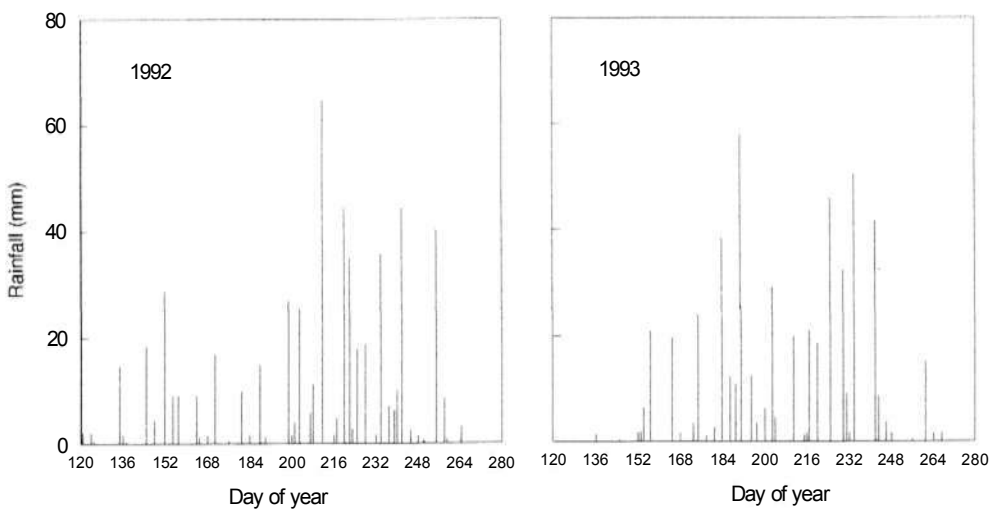

Fig. 1. Rainfall amount and distribution at ICRISAT Sahelian Center in 1992 and 1993.

Table 1. Dates (days of the year) of phenological stages for three pearl millet varieties, as affected by P-fertilizer addition, at ICRISAT Sahelian Center in 1992 and 1993.

		Variety					
		Sadore		ITMV		ICMV1S	
Phenol.	P-treatment	Locale		8001		85327	
Stage	(kg P_2O_5 ha^{-1})	1992	1993	1992	1993	1992	1993
Sowing	0	153	166	153	L66	153	166
	30	153	166	153	166	153	166
Booting	0	211	222	204	217	204	217
	30	211	217	204	217	204	217
Head	0	230	237	224	229	224	229
Emergence	30	218	231	218	224	218	224
50%	0	236	245	230	236	230	236
Flowering	30	232	243	225	230	225	230
Maturity	0	260	272	260	261	260	261
	30	260	272	260	261	260	261

Root growth

Root length density data are presented for different depth layers in Figure 2 for 1992 and in Figure 3 for 1993. Absolute values for RLD are similar to those reported by Azam-Ali et al. (1984) and Bieler (1992), but are considerably lower than those reported by Hafner et al. (1993a). We attribute these differences to methods of washing and separation of live and

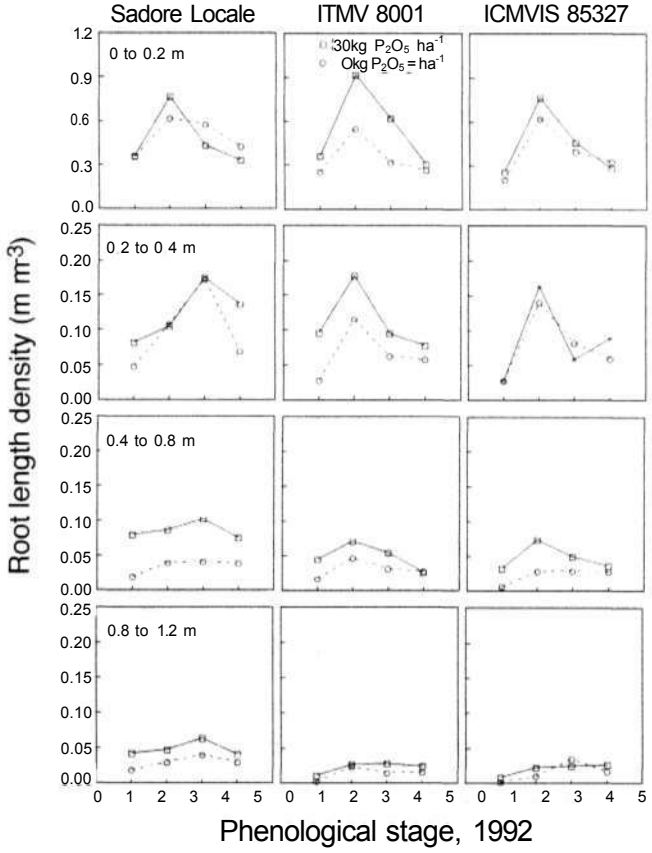

Fig. 2. Root length density (RLD) of three pearl millet varieties in different soil depth layers, as affected by P-fertilizer, at ICRISAT Sahelian Center, 1992 and 1993.

dead roots.

The most prominent trend in Figures 2 and 3 is that the greatest RLD values were found in the upper 0.20 m of the soil profile, consistent with other field studies of pearl millet conducted during the rainy season (Chopart 1983; Cisse and Vachaud 1988; Payne et al. 1990; Hafner et al. 1993a) and dry season (Azam-Ali et al. 1984). Several authors (e.g., Geiger et al. 1992a, b; Hafner et al. 1993b) have shown that almost all available plant nutrients in these soils are located in the upper 0.20 m. The pronounced plant investment into root growth in this layer relative to lower layers, where greater water reserves are generally located, suggests that the rooting patterns of pearl millet have at least as much to do with nutrient distribution as they do with water distribution.

In both 1992 and 1993, root growth in the upper 0.20 m soil layer was maximal between booting and head emergence; thereafter, growth was greatly reduced. Chopart (1983) reported a similar trend. In 1992, growth patterns were similar for ICMVIS 85327 and ITMV 8001 in the next two depth layers, i.e., 0.20-0.40 m and 0.40-0.80 m. However, the landrace had maximal growth in these depth layers between head emergence and flowering. The landrace tended to have higher RLD than did the other two varieties at lower depth layers, especially when P was applied.

In most depth layers, there was a pronounced increase in RLD due to P-application in both years. Similarly, Cisse and Vachaud (1988) reported large increases in root growth due to manure and lime application. Relative changes in root counts at flowering (Table 2)

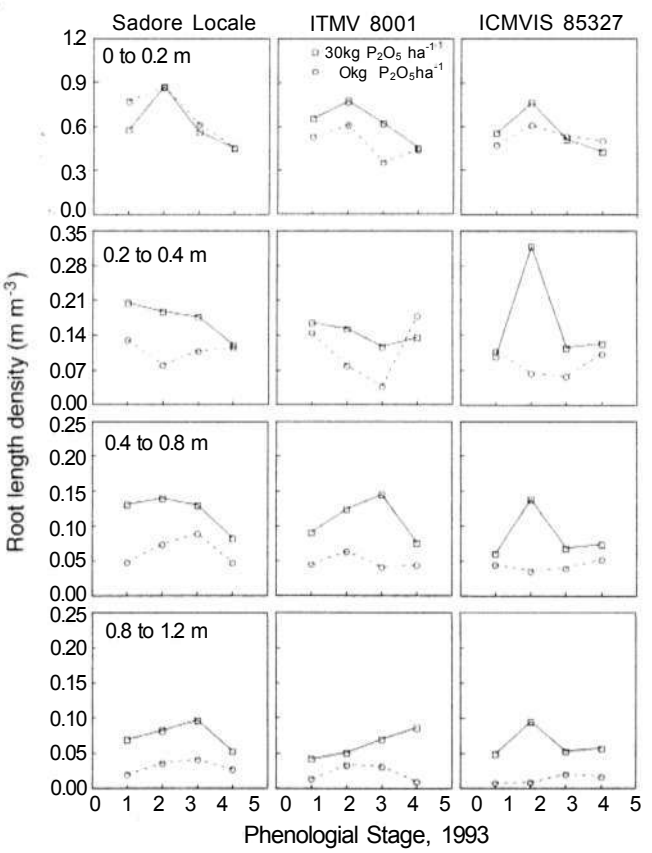

Fig. 3. Root length density (RLD) of three pearl millet varieties in different soil depth layers, as affected by P-fertilizer, at ICRISAT Sahelian Center, 1992 and 1993.

Table 2. Relative change in root counts at different soil depths during flowering as affected by P-application for three pearl millet varieties grown at ICRISAT Sahelian Center in 1992 and 1993. NA, not applicable (No root sampling from 1.2 to 1.8 m soil depth in 1992).

Variety	Depth Interval (m)	Relative Change 1992	1993
Sadore	0-0.2	-0.25	-0.10
Locale	0.2-0.4	+0.01	+0.63
	0.4-0.8	+1.40	+0.47
	0.8-1.2	+0.57	+1.32
	1.2-1.8	NA	+1.04
ITMV	0-0.2	+0.95	+0.76
8001	0.2-0.4	+0.52	+2.01
	0.4-0.8	+0.75	+2.60
	0.8-1.2	+0.88	+1.20
	1.2-1.8	NA	+1.25
ICMVIS	0-0.2	+0.16	-0.04
85327	0.2-0.4	-0.29	+0.99
	0.4-0.8	+0.68	+0.74
	0.8-1.2	-0.28	+1.55
	1.2-1.8	NA	+1.78

suggest that root growth of the variety ITMV 8001 increased considerably due to P-application in the upper 0.20 m of soil during both years, whereas Sadore Locale showed no increase in this layer. Root response for the variety ICMVIS 85327 was varied. Relative increases in RLD tended to be greater in the deeper layers for all varieties, especially in 1993.

Such increases in root growth due to phosphate application could be advantageous for soil water extraction during dry periods or periods of high water demand, because the resistance to water uptake in any soil layer is inversely proportional to the length of root in that layer (Campbell 1985). This hypothesis was evaluated from soil water content data for different depth layers during the two seasons for the variety ITMV 8001, because it showed the largest root growth response in the upper two layers to added-P (Figs 2 and 3).

Soil water content

Soil water content for the two P-treatments (Fig. 4) was often similar in the various layers during the two seasons, except during drying cycles induced by low rainfall or high plant demand. During these periods, soil water content tended to be less for plots that received P-fertilizer. This was particularly evident around 200 DOY in 1992, especially for the depth layer 0.4-0.8 m. In 1993, dry spells occurred between 200 and 220 DOY, and toward the end of the season. Some increased root extraction is suggested during these periods, especially from the layer 0-0.20 m. There is no strong evidence of increased water extraction during the last drying cycle in the lower two layers, which may be due to lowered water demand associated with senescent plants, or sufficiently available reserves in the upper soil layers. Soil water content data for the other varieties were fairly similar (data not shown).

Data in Figure 4 suggest that increased soil water extraction was more prominent in upper soil layers than in lower layers, but 1991 and 1992 represent relatively mild years in

terms of drought. Generally, it is considered that water is taken from lower soil layers with fewer roots only after the upper layers with more roots become sufficiently dry (Campbell 1985). Payne et al. (1990) reported that pearl millet extracted all plant available water within and immediately below its root zone during a severe drought year (1985) in Chikal, Niger, despite the low number of roots in lower layers.

Other than during occasional drying cycles in 1992 and 1993, average soil water contents tended to be similar between P-treatments. We believe this is due to the fact that within both years, ET was little affected by fertility treatments (Table 3), implying that similar amounts of water infiltrated the soil profile. pearl millet plants receiving no P tended to have lower leaf area, which increases partitioning of ET into soil evaporation (Ritchie 1983), and decreases its partitioning into crop transpiration, which is directly related to root extraction of water. This effect of fertility on the partitioning of ET explains in a large part why it is difficult to predict pearl millet yield from ET in the Sahel (Cisse and Vachaud 1988; Klaij and Vachaud 1988; Payne, in press), unless separate relations are distinguished for different classes of soil fertility (Forest et al. 1990; Payne, in press). In sandy soils, the rate of soil evaporation becomes almost negligible after the first few days of a dry spell (Hillel, 1992). Thereafter, any continued ET is due mostly to crop transpiration. It is during these spells that evidence of root extraction of soil water is most easily observed.

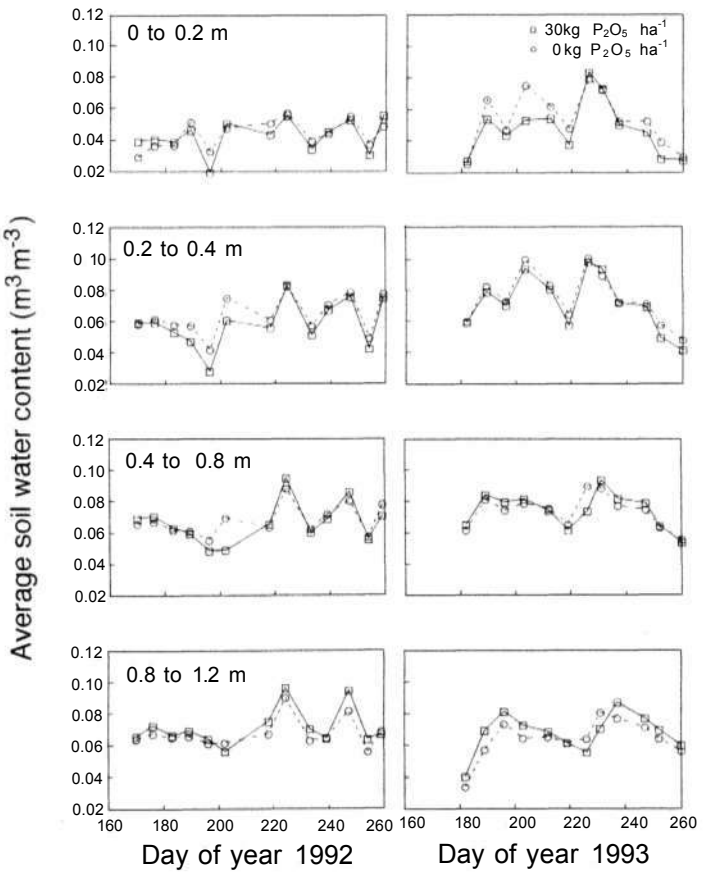

Fig. 4. Soil water content for different depth layers, as affected by P-fertilizer, for one pearl millet variety at ICRISAT Sahelian Center, 1992 and 1993. Data for other varieties were similar.

Table 3. Seasonal crop and soil evaporation (ET) as affected by P-application of three pearl millet varieties grown at ICRISAT Sahelian Center in 1992 and 1993.

Variety	P-treatment (kg P_2O_5 ha^{-1})	Total ET(mm) 1992	1993
Sadore	0	384	413
Locale	30	351	383
ITMV	0	374	374
8001	30	368	363
ICMVIS	0	378	387
85327	30	376	387
Standard Error	33	21	

Conclusion

Results of this 2-year study on pearl millet root growth show that soil nutrient availability cannot easily be separated from water availability because of it effects upon root growth, which in turn determines plant supply and use of soil water. Root growth was greatest from booting to head emergence in the upper 0.20 m of the soil profile, where almost all soil nutrients were located. Although there were minor genotypic differences in rooting habits, all varieties increased root growth in most soil layers when P was applied. The greatest relative increases in root growth were in the deeper soil layers, from which soil water reserves are taken up by crops during dry spells. Greater root growth in these deeper layers permitted increased soil water extraction during dry spells. Little evidence of increased soil water extraction due to added-P could be found during wetter periods. We attributed this lack of increased water extraction during wet period to increased partitioning of ET to soil evaporation due to lower leaf area in plots of low nutrient status.

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Effects of Fertilizer Nitrogen and Irrigation on Root Growth, and Water Uptake with Special Reference to Postrainy Season Sorghum

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Abstract

Effects of fertilizer nitrogen (N) and irrigation on root development are discussed by collating the observations in published reports with those in our study using field-grown sorghum [Sorghum biocolor (L.) Moench] on a deep Vertisol in semi-arid tropical India. In our study, the total root biomass was affected by fertilizer-N and irrigation and by their interaction. It is the top soil layers that contribute largely to increased root biomass due to fertilizer-N and irrigation. These observations agree with those in other reports. The total root length was not significantly affected by fertilizer-N, but was consistently higher under dry conditions than under irrigated conditions. Spatial distribution of root length did not fit a simple mathematical model such as linear, exponential or logistic curve, except at very young growth stages under irrigated conditions. Except the top 16-cm layer, the depth at which root length density zvas maximum shifted to deeper layers as sorghum grew. This may indicate that some roots die after water extraction and that new roots grow at the soil layers where water zvas available. This specific feature would contribute to the complexity of modeling of root development. Rooting depth was not affected by fertilizer-N, but it was consistently greater under dry conditions than under irrigated conditions. The root depth had a linear relationship with time under dry and irrigated conditions up to the physiological maturity stage. Water uptake by sorghum was determined as the difference between measured evapotranspiration and estimated soil evaporation. In non-irrigated treatment, the differences in water uptake among N treatments were not significant. In the irrigated treatment, the rates of 30 to 150 kg N ha (30 N and 150 N, respectively) resulted in significantly higher water uptake than no fertilizer-N. The fertilizer-N effect in our study zvas not as clear-cut as that in other reports.

Introduction

The spatial and temporal development of roots in coordination with the development of the shoot largely determine soil water extraction and nutrient uptake. The size and pattern of

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root development are particularly important for crops growing in soil that supplies only limited quantities of water and nutrient in time and space.

In semi-arid tropical India, postrainy season sorghum is grown on Vertisols where the fertilizer applied near the soil surface is absorbed by sorghum only to a limited extent. In such an environment, it is necessary to study the effect of fertilizer on root growth in combination with the effect of soil water. In postrainy season, 1988, at the ICRISAT Asia Center (IAC), we initiated an experiment with sorghum in which root growth and extension were monitored under dry and irrigated conditions and with different N levels. Here, we discuss fertilizer-N and irrigation effects on root development by collating our observations with other published observations.

Root biomass

In our study, during the postrainy season with sorghum [*Sorghum bicolor* (L.) Moench] hybrid "SPH280", total root biomass increased almost linearly up to the dough stage, i.e., 93 days after emergence (DAE), and then nearly leveled off or declined both under dry and irrigated conditions (Fig. 1). A significant fertilizer-N effect on total root biomass was found throughout the growth duration. However, the extent of this effect was not always proportional to N-dose rate.

Overall, the pooled total root biomass across all N rates showed a trend of being always higher (except 31 DAE) under irrigated conditions than under dry conditions (Fig. 1). Interactive effects of fertilizer-N and irrigation were observed only at 93 DAE, when combined effects of both were higher than their additive effects.

Irrespective of irrigation treatment, a large part of the root biomass was found in the top layer of soil (0 to 0.1 m) (Table 1). It ranged from 32% to 41% of total root biomass across-N levels and irrigation treatments. Within the dry treatment, there was no significant difference in root biomass of the top layer between N-levels. Within the irrigated treatment, the rates of 60 to 150 kg N ha^{-1} produced significantly greater root biomass at the top layer than the zero N and 30 kg N ha^{-1} rates (0 N and 30 N, respectively). At a 1.80 m-depth (1.725 m to 1.875 m), there was a significant fertilizer-N effect. The two adjacent layers, 1.65 and 1.95 cm, had a similar trend. However, the root biomass at these layers comprises only a small portion of the total root biomass.

The ratio of root to total biomass was greater during early growth stages than during later growth stages irrespective of fertilizer-N levels or irrigation treatments (Table 2). At 31 DAE, this ratio under dry conditions was the highest, at about 30% of total biomass, and it was the highest at the zero N rate. Highly significant fertilizer-N effects were observed at 31, 45, and 59 DAE, and the 0 N rate produced the highest ratio irrespective of irrigation treatment. The root-total biomass ratio rapidly declined up to 59 DAE (booting stage), and then it leveled off until harvest. At 93 DAE (physiological maturity) and at harvest, the root-total biomass ratio did not differ among different N-levels or between irrigation treatments.

Meyers (1980) observed that the above-ground biomass varied with fertilizer levels, whereas the root biomass varied very little with fertilizer levels. Brown et al. (1987)

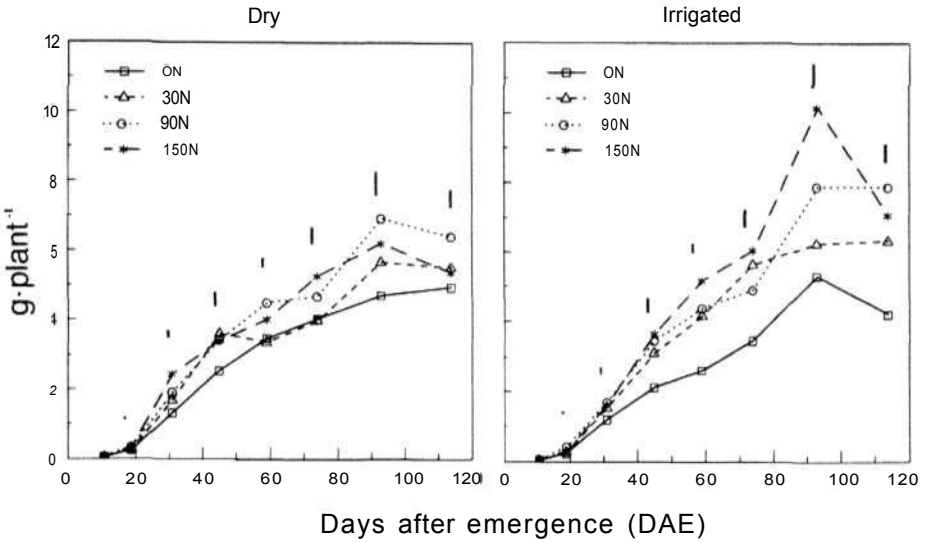

Fig. 1. Effects of irrigation and fertilizer-N on total root biomass. The bars are standard errors of means to compare fertilizer-N effects within an irrigation level at a particular growth stage.

Table 1. Root biomass as a function of soil depth at the time of maximum total root biomass, 93 DAE.

	N-level				SE[2]		
	ON		150N				
Depth(m)	Dry	Irrigated	Dry	Irrigated	Irrigated[3]	Nitrogen[4]	Irrigated[5]* Nitrogen[5]
			g m^{-2}				
0.05	26.9 (34)	31.9(36)	41.3 (40)	69.7(41)	0.43	4.43 **	7.05
0.16	6.0 (8)	10.5 (12)	8.5 (8)	16.1 (10)	0.70 *	0.98!	1.44
0.30	5.6 (7)	8.2 (9)	6.3 (6)	7.8 (5)	0.40 !	0.80	1.11
0.45	4.4 (6)	4.4 (5)	5.3 (5)	6.6 (4)	0.37	0.39!	0.63
0.60	5.2 (7)	3.9 (4)	3.6 (3)	8.6 (5)	0.77	0.88	1.38
0.75	5.6 (7)	4.8 (5)	4.0 (4)	8.4 (5)	0.37 *	1.54	2.01
0.90	3.3 (4)	4.4 (5)	2.5 (2)	7.7 (5)	0.58	0.91	1.31
1.05	3.4 (4)	3.9 (4)	4.1 (4)	8.1 (5)	0.29	0.63	0.87
1.20	3.5 (4)	5.0 (6)	6.1 (6)	9.1 (5)	0.19!	0.79	1.04
1.35	3.1 (4)	4.3 (5)	4.6 (4)	8.6 (5)	0.34	0.98	1.31
1.50	4.0 (5)	4.3 (5)	4.2 (4)	8.9 (5)	0.40	0.92!	1.25
1.65	3.7 (5)	1.9 (2)	5.1 (5)	4.5 (3)	0.26	0.73 !	0.98
1.80	1.8 (2)	0.7 (1)	4.4 (4)	3.6 (2)	0.38!	0.73*	1.01
1.95	1.7 (2)	0.2 (0)	3.3 (3)	1.7 (1)	0.70	0.51 !	0.96
Total	78.1(100)	88.6(100)	103.3(100)	169.3(100)	6.31 !	7.96 ***	12.08 !

1 The values in parentheses are percent of total root biomass.
2 Standard error or means calculated from all treatments in this study;!, *, ** and *** significant at P = 0.1, 0.05, 0.01 and 0.001 respectively.
3 For irrigation effect comparison.
4 For N-fertilizer effect comparison..
5 For interactive effects of irrigation and fertilizer-N comparison.

Table 2. Effect of irrigation and fertilizer-N on the ratio of root to total biomass.

N level	Days after emergence							
(kg ha^{-1})	11	19	31	45	59	74	93	114
Dry								
0	0.26	0.25	0.34	0.27	0.18	0.12	0.10	0.10
30	0.27	0.23	0.30	0.24	0.15	0.09	0.11	0.10
60	0.24	0.22	0.32	0.22	0.13	0.12	0.10	0.09
90	0.29	0.27	0.28	0.20	0.14	0.11	0.11	0.10
120	0.27	0.24	0.25	0.21	0.12	0.13	0.12	0.10
150	0.26	0.26	0.32	0.20	0.12	0.10	0.10	0.10
Mean	0.27	0.24	0.30	0.22	0.14	0.11	0.11	0.10
Irrigation								
0	0.26	0.27	0.35	0.32	0.20	0.13	0.10	0.10
30	0.27	0.20	0.27	0.23	0.12	0.11	0.08	0.10
60	0.24	0.24	0.24	0.20	0.14	0.08	0.11	0.09
90	0.29	0.25	0.24	0.19	0.12	0.10	0.10	0.09
120	0.27	0.22	0.22	0.15	0.10	0.10	0.10	0.09
150	0.26	0.22	0.21	0.17	0.13	0.09	0.10	0.09
Mean	0.27	0.23	0.26	0.21	0.13	0.10	0.10	0.09
SE(1)	±0.039	±0.021	±0.017**	±0.026**	±0.013**	±0.010	±0.010	±0.012
SE(2)		±0.007	±0.005**	±0.018	±0.010	±0.001	±0.005	±0.006

SE(1): To compare N level; SE(2): To compare irrigation.
**: Significant difference at the 0.01 level.

observed that at maturity, fertilizer-N had little effect on root-to-total plant weight ratios of barley, which indicates that root biomass production responded to fertilizer similarly to above-ground biomass production. On the contrary, a reduction in root biomass of grain sorghum was observed with measuring fertilizer-N when compared with that of an unfertilized control (Roder et al. 1989). In our study, a highly significant effect of fertilizer-N on the root biomass was observed. It is the shallow soil layers that largely contribute the effects on total root biomass production. The equal responsiveness of the root biomass and the above-ground biomass production to fertilizer-N was also supported by the ratio of root biomass to total biomass around the maturity stage of sorghum. Although our observation leads us to believe that root biomass production responded positively to fertilizer-N, it is possible that root growth characteristics differ with crop species, cultivars, soil conditions and climatic factors.

Compared with the information on the effect of fertilizer-N on root biomass production, less information is available on the effect of irrigation or soil water on root biomass production under field conditions. Kaigama et al. (1977) reported for field grown grain sorghum that a major difference between irrigated and nonirrigated treatments was the increased quantity of irrigated roots in the top 15 cm of soil. A greater proportion of total root dry matter accumulated at the deeper depths in nonirrigated than in the irrigated sorghum. However, the increased quantities at the deeper depths are far less than those at the shallower depths. Gairi and Prihar (1985) also reported that the root weight density *(fig*

root cm^{-3} soil) of field grown wheat in upper layers increased due to irrigation in sandy loam soil. As our study demonstrated, it is the root biomass in the top 0.3 m of soil that greatly increased due to irrigation, and increased root biomass was not generally observed at the deeper depths, although there were some layers at which statistically significant but small increases in root biomass were observed. In terms of increased quantity, our observation is in agreement with those of Kaigama et al. (1977) and Gajri and Prihar (1985).

Root length

It has been reported that fertilizer-N and irrigation affect root length of various crops. For example, application of N and P fertilizers increased the total root length of barley (Brown et al. 1987). Total root length was significantly increased by N-fertilizer (67 kg N ha^{-1}), but high rates of N-fertilizer (134 kg N ha^{-1}) decreased the total root length (Comfort et al. 1988). The total soybean root length was affected by drought stress and irrigation treatments and significantly increased by irrigation treatment (Hoogenboom et al. 1987). Gajri et al. (1989) also observed an increase in root length index (km root m^{-2} surface area in the rooted profile) of wheat, which is comparable to total root length.

In our study with field-grown sorghum, both under dry and irrigated conditions, total root length increased up to 93 DAE and then declined at harvest (Fig. 2). Only at 59 DAE and at harvest there were differences in total root length among N-levels. A significant irrigation effect on total root length across N-levels was observed only at 31 DAE and at harvest. Overall, the roots tended to increases their total length more under dry conditions than under irrigated conditions throughout the growth duration, while roots tended to have less biomass under dry conditions as mentioned earlier. No interactive effects of fertilizer-N and irrigation on total root length were found throughout the growth duration.

Although total root length was affected by N-fertilization and irrigation at some growth stages, it can be contemplated that effects of N-fertilization and irrigation at upper soil layers may be different from those at lower layers because fertilization and irrigation treatments are applied to the top layers of soil. The effect of irrigation on root length density in the soil profile was different between the layers above and below 0.45 m (Fig. 3). After 59 DAE, the root length densities in the top layers at the zero N rate were greater under irrigated conditions than under dry conditions. Such an irrigation effect was more obvious at the rates of 30, 60, and 90 kg N ha^{-1} (30 N, 60 N and 90 N, respectively) (data not shown), but less obvious for the rates of 120 and 150 kg N ha^{-1} (120 N and 150 N, respectively). Unlike root length densities in the top three layers, the ones at depths below 0.45 m were greater under dry conditions than under irrigated conditions, which depends on the depth and the growth stage. At 31 DAE, the root length density under dry conditions was significantly greater than under irrigated conditions only at upper to middle depths (0.30 to 0.60 m). As the plant grew older, such significant differences shifted to the middle depth, the depth of lower middle, and then to the lower depth. Root length density was not affected by fertilizer-N application as much as root biomass.

Comfort et al. (1988) found that root length was significantly increased in the top 0.3 m by applying 67 kg N ha^{-1} but remained the same or decreased at 134 kg N ha^{-1}

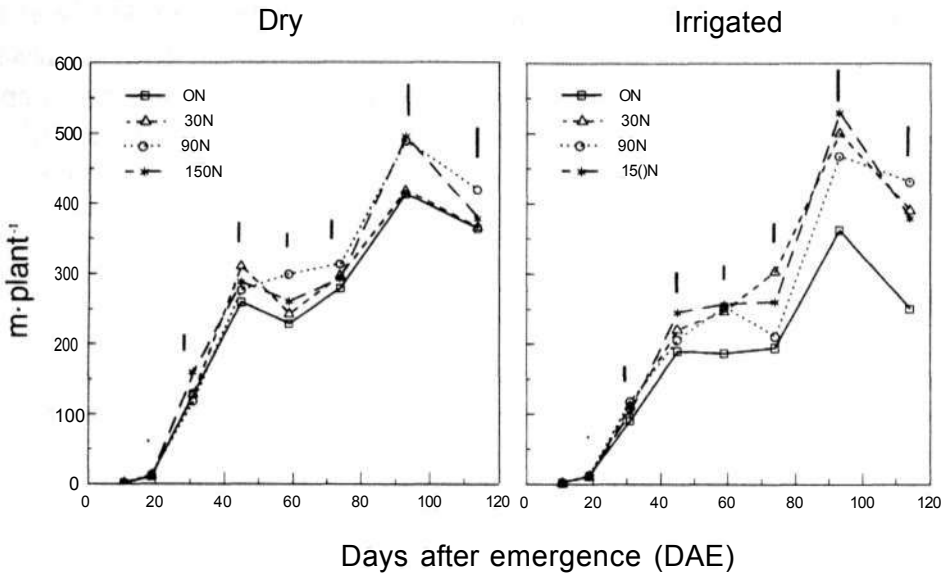

Fig. 2. Effects of irrigation and fertilizer-N on total root length. The bars are standard errors of means to compare fertilizer-N effects within an irrigation level at a particular growth stage-

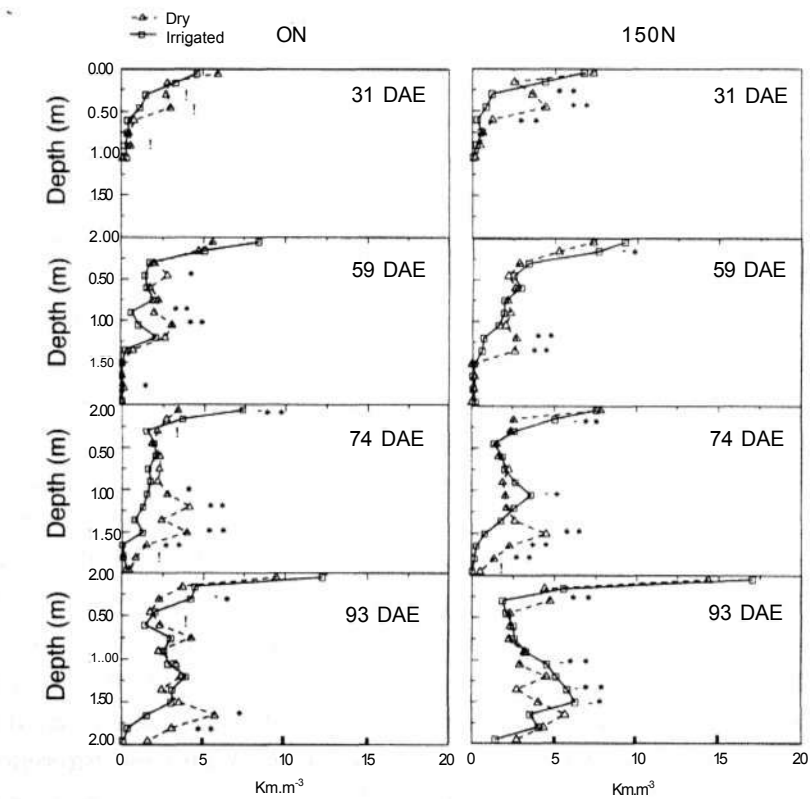

Fig. 3. Root length density as a function of depth for sorghum at the rates of zero N and 150N kg ha^{-1}. The denotation (i), (*) and (**) indicates significant difference at the 10%, 5% and 1% levels respectively, and those accompanied by a minus sign indicate that the irrigation had a significantly higher value. DAE = Days after emergence.

Hoogenboom et al. (1987) observed with soybean that irrigation mainly increased the roots in soil layers above 0.6 m, whereas roots under drought stress conditions penetrated deeper soil layers below 0.6 m. In our study, fertilizer-N increased the root biomass in the top 0.45 m but did not increase the root length. The soil in our study contained about 14 ppm mineral-N before fertilizer-N treatments were applied. We surmise that root length is less sensitive to changes in mineral-N of the soil, and therefore root length did not respond to fertilizer-N applications in the soil of this study. In the 1989/90 postrainy season four sorghum genotypes were examined for their response to fertilizer-N application under dry conditions in another deep Vertisol that contained 7 ppm mineral-N. Root length density in all four genotypes positively responded to fertilizer N application (data not shown). This result supports our conclusion of a more conservative response of root length to fertilizer-N application.

Rooting distribution curve

Gerwitz and Page (1974) obtained a linear relationship for various crops between the soil depth and the logarithms of root percentage of whole root systems within a depth. An exponential distribution with depth has often been reported (e.g., Gregory et al. 1978). Belford et al. (1987) observed that the distribution with depth of nodal and tiller roots of winter wheat was exponential, but that of seminal root was linear.

In our study, the root distribution did not seem to depict a model curve, except the root distribution of young roots (up to 31 DAE) in the irrigated treatment. Except for the top 0.16 m layer, there were layers where root length density was greater than adjacent layers. These layers were more distinct in dry treatment (Fig. 3), and moved down to deeper soil depth with growth stages. We surmise that this phenomenon is due to the death of some roots after water uptake at particular layers and to the growth of new roots at deeper layers where the roots are absorbing water. Blum and Ritchie (1984) proposed that the soil surface moisture controls the number of crown roots and subsequently root distribution along the soil profile. It is also possible in our study that the drier soil surface caused compensatory increased root elongation in deeper soil layers.

Rooting depth

In our study with sorghum, rooting depth, the depth of containing 90% of the roots, increased with growing period up to 93 DAE (maturity) and then leveled off at harvest (Fig. 4). The rooting depth increased almost linearly up to 93 DAE. There was no significant difference in rooting depth between N levels. Up to 31 DAE, differences in rooting depth were not observed between dry conditions and irrigated conditions except at 60 N (data not shown). After 31 DAE, rooting depth was consistently greater under dry conditions than under irrigated conditions.

Borg and Grimes (1986) showed that time course of rooting depth can be described by a sine function. The rooting depth with time in our study may fit a sine function with

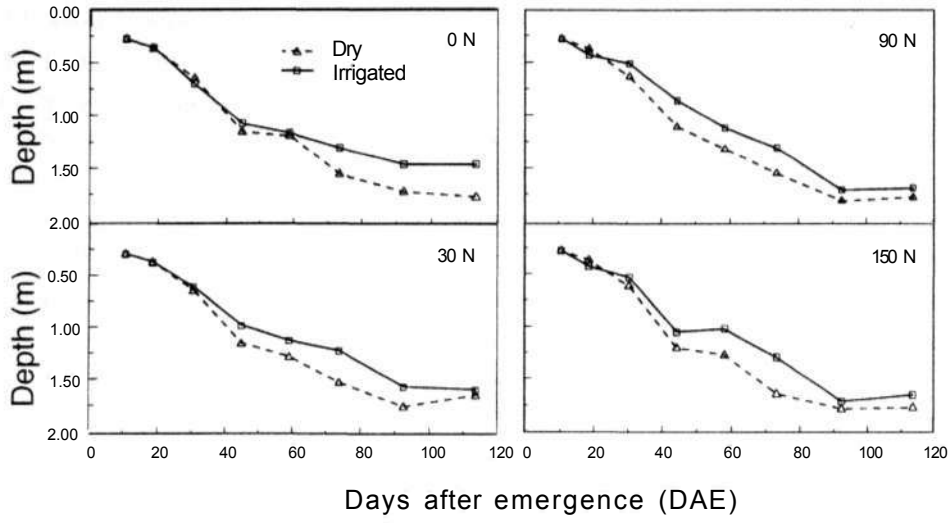

Fig. 4. Changes of root depth, the depth of the soil containing 90% of the root, with growth stages for sorghum grown at the rates of 0, 30, 90 and 150 kg N ha^{-1} under dry and irrigated conditions.

certain errors if the root depth data at harvest (114 DAE) are included. However, a linear function also fits if the data at harvest are not included, because the root growth ceased at 94 DAE (physiological maturity). Assuming that root depth increase linearly with growing days, the rate of root depth ranges from 1.9 to 2.0 cm day^{-1} under dry conditions and from 1.5 to 1.8 cm day^{-1} under irrigated conditions.

Soil moisture and water uptake

The plants grow and survive by coordinating the operation of roots and shoots. Both irrigation and fertilizer-N application influence the canopy size, root length, and rooting depth, and consequently influence seasonal water use by the plants. A much larger combined effect of fertilizer-N and irrigation than the sum of their separate effects was observed with wheat (Gajri et al. 1989). Comfort et al. (1988) described that high rates of N-fertilization may inhibit deeper root growth and hence potentially decrease the use of deeper soil water reserves.

We measured soil water content in the field planted with sorghum during the 1988/89 postrainy season, and then estimated the evapotranspiration from the change in soil water content, the amount of irrigation and the amount of precipitation. Soil evaporation was calculated using the soil water balance model of Ritchie (1972). Transpiration was calculated as the difference between observed evapotranspiration and soil evaporation.

Changes in soil moisture in soil profile as the plants grew were greater in irrigated conditions than in dry conditions (Fig. 5). Within an irrigation treatment, changes in soil

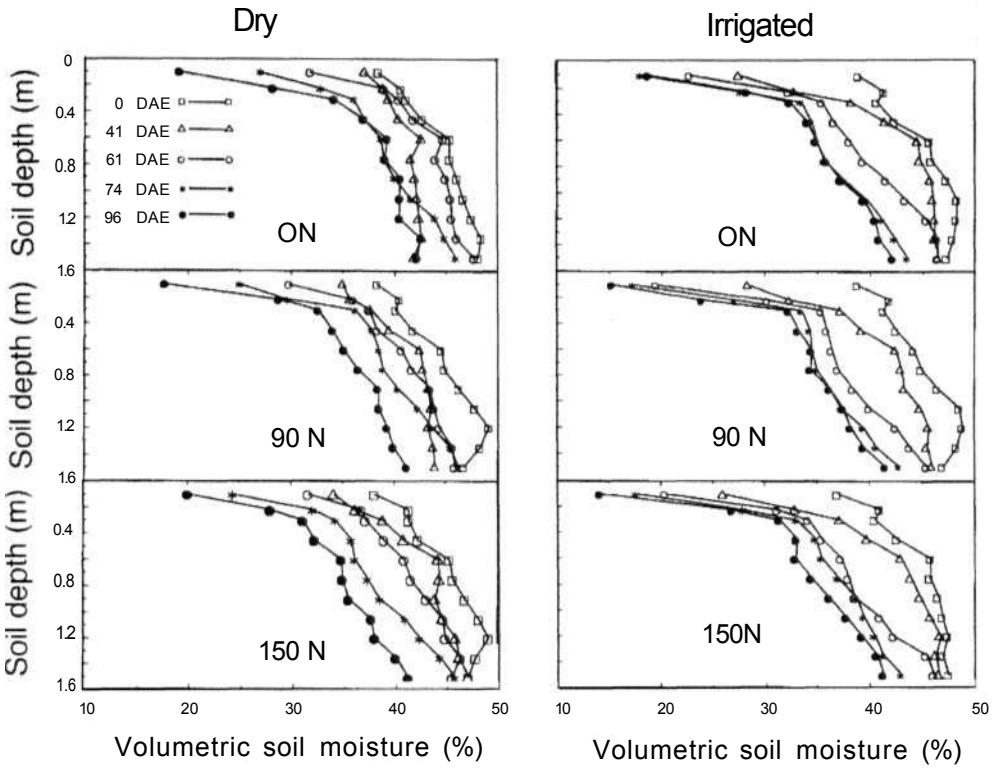

Fig. 5. Soil moisture as a function of depth for sorghum at the rates of 0, 90 and 150 kg N ha^{-1} under dry and irrigated conditions.

moisture increased with fertilizer-N levels. These data indicate that sorghum plants suffer from moisture stress in dry conditions and that increasing biomass production of sorghum with fertilizer-N levels demanded more water.

Water uptake was greater in the irrigated treatment than in the dry treatment at all nitrogen levels (Table 3). In the dry treatment, water uptake increased with N-fertilizer application up to 60 N, and beyond this N-level it did not differ significantly. In the irrigated treatment, the increases in water uptake were observed up to 30 N and beyond this N-level the water uptake did not increase significantly. Water uptake is not controlled by root growth alone, but by coordinated function of root and shoot growth. However, increased root length in corresponding treatments can increase the capacity of water uptake. The observation in our study shows that increased root length due to fertilizer-N or irrigation increased water uptake by field-grown sorghum, but interactive effects of fertilizer N and irrigation were not observed.

Conclusion

The effects of fertilizer-N and irrigation on root biomass, root length, root depth, and water uptake of field-grown sorghum were investigated on a deep Vertisol during the postrainy

Table 3. Effects of irrigation and N fertilizer on evapotranspiration, transpiration, and soil evaporation in various treatments.

N level (kg ha^{-1})	Evapotranspiration (mm)		Transpiration (mm)		Soil evaporation (mm)	
	Dry	Irrigation	Dry	Irrigation	Dry	Irrigation
0	199	367	151	273	48.6	94.5
30	202	397	154	308	48.7	89.5
60	237	392	188	306	48.6	85.3
90	220	379	172	295	48.5	84.4
120	201	416	152	331	48.5	85.0
150	195	396	147	314	48.5	82.4
SE(1)	15.6		15.89		0.92	
SE(2)	17.9		17.87		0.93	

SE(1): To compare N level; SE(2): To compare irrigation.

season. These results were collated with those in other reports. The responses of total root biomass and root biomass distribution with soil depth were consistent with those in other published reports. The root depth under dry and irrigated conditions increased linearly with time. Therefore, these root parameters can be readily modeled by using or modifying existing models. On the other hand, the length distribution with soil depth in our study does not seem to fit well to existing mathematical models. This length distribution may has to be taken into account for modeling of root development, which will be the case for modeling of water uptake because root length distribution is closely related to water uptake.

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Effects of Transient Waterlogging and Nitrogen Top-Dressing on the Shoot and Root Growth of Short-Duration Pigeonpea

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Abstract

Recovery of the shoot and root growth of short-duration pigeonpea from transient waterlogging damage was measured with or without nitrogen (N) top-dressing to determine the effectiveness of N top-dressing in alleviating the waterlogging damage.

Root growth was severely impaired at the pre-flowering stage by transient waterlogging in both shallow and deep soil layers (i.e., nearly 50% reduction) in a Vertisol. Crop growth rate (CGR) was also significantly depressed during the subsequent recovery period, when branch roots were produced mainly in the shallow soil layer and the root distribution became shallow. Enhancement of root respiration rate and specific nodule activity after waterlogging indicates that the root system can partially rejuvenate during the recovery period, though it was not enough to compensate for the waterlogging damage. Nitrogen top-dressing, especially, application of 50 kg N ha^{-1}, was very effective in allowing rapid recovery of shoot and root growth from waterlogging damage, because short-duration pigeonpea suffered from N deficit after transient waterlogging. The CGR of waterlogged pigeonpea was enhanced significantly with N top-dressing. Meanwhile, an increase in root length density with N top-dressing was observed not only in the shallow soil layer but also in the deep soil layer. This promotion is a possible consequence of enhanced shoot growth or vice versa. These results show that active formation of branch roots near the soil surface after transient waterlogging would assure reliable N-uptake in the plants of short-duration pigeonpea, leading to quick recovery of shoot and root growth, and subsequently to improve grain yield.

Introduction

In India, nearly 6 million hectares of land, especially Vertisols, are prone to waterlogging during the rainy season (Chauhan 1987). According to an agroclimatological study of Reddy and Virmani (1981), waterlogging is a major constraint to rainy season crops on soils with high water-holding capacity, such as Vertisols. Although short-duration pigeonpea (4-

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5 months to maturity) is being increasingly used in India because of the high potential for developing new and productive cropping systems (Panwar and Yadav 1981; Kumar Rao and Dart 1987; Troedson et al. 1990), this type of pigeonpea may have a higher possibility of facing waterlogging at critical growth stages due to its early phenology, as compared with medium- (5-6 months) or long-duration (6-9 months) pigeonpea. Leguminous crops are very susceptible to waterlogging at the pre-flowering stage (Minchin et al. 1978; Cannell et al. 1979; Sugimoto et al. 1988a). There is normally insufficient time for recovery to produce potential seed yield in short-duration pigeonpea.

In cereal crops, waterlogging restricts seminal root growth, causes a breakdown of the root tissues and reduces root mass. In contrast, it promotes the formation of nodal roots from the shoot base in wheat (Trought and Drew 1980), oats (Cannell et al. 1985), sorghum (Pardales et al. 1991), and barley (Cannell et al. 1984). Few studies have reported the effect of waterlogging on the root distribution in field-grown leguminous crops (Cannell et al. 1985; Matsunaga et al. 1994).

Depression of N-uptake after waterlogging limits the growth and grain yields of cereal crops (Watson et aL 1976; Cannell et al. 1985; Veen 1988), and soybean (Nathanson et al. 1984; Sugimoto et al. 1988b). Therefore, N-application can compensate partially or completely for the reduction of grain yield due to waterlogging damage by promoting tillering in cereals or increasing the rate of photosynthesis in soybean, or both (Watson et al. 1976; Cannell et al. 1985; Veen 1988; Sugimoto et al. 1989). There have, however, been few reports on the influence of N-application on waterlogged pigeonpea (Matsunaga et al. 1992, 1994).

Experimental site, treatments, and observations.

Short-duration pigeonpea (*Cajanus cajan* (L.) Millspaugh cv. ICPL 87) was sown on a Vertisol at ICRISAT Asia Center in mid-June soon after the onset of the rainy season during the 1990 to 1992 seasons.

Three days of waterlogging were imposed at the pre-flowering stage in August when leguminous crops are very susceptible to waterlogging (Minchin et al. 1978; Cannell et al. 1979; Sugimoto et al. 1988a). In 1990, N-fertilizer was applied to each subplot, at the rates of 0, 25, or 100 N kg ha^{-1}, as a basal fertilizer with single superphospate (SSP). In 1991 and 1992, N-fertilizer was top-dressed at 1 day after the termination of waterlogging (DAW). The N-application rates were 0, 50, and 100 kg ha^{-1} in 1991 and 0 and 50 kg ha^{-1} in 1992.

Shoot dry mass and leaf chlorophyll concentration were measured at 10 to 14 DAW. Vertical root distribution in the soil was measured by a pit-excavation method (Matsunaga et al. 1992) and an auger sampling method after waterlogging treatment (Matsunaga et al. 1994). Nodule activity and root respiration was determined by acetylene reduction assay, and oxygen analyzer, respectively, using roots and nodules recovered by a soil-root monolith method (Matsunaga et al. 1992,1994).

Shoot growth after waterlogging

Short-duration pigeonpea is severely damaged by transient waterlogging, resulting in yellowing of the entire canopy followed by senescence and abscission of lower leaves (Chauhan 1987). In our study, leaf area was significantly decreased by transient waterlogging, and chlorophyll and N concentrations in the remaining leaves were also significantly reduced at 1 DAW (Table 1). Obviously the symptom is attributable to shortage of N-supply to plants (Matsunaga et al. 1992, 1994), and this N-stress prevents short-duration pigeonpea from quick recovery. Therefore, crop growth rate (CGR) of waterlogged plants was much lower than that of control plants during the subsequent recovery period, unless N-fertilizer was applied (Table 2).

Top-dressing with 50 kg N ha^{-1} was most efficient in increasing the depressed CGR. Sufficient soil moisture after waterlogging should be favorable for pigeonpea to absorb applied N-fertilizer (Burford et al 1989).

Table 1. Effect of waterlogging on leaf chlorophyll and nitrogen, and leaf area at 1 day after termination of waterlogging.

Year	Treatment	Chlorophyll (mg m^{-2})	Nitrogen (g kg^{-1})	Leaf area (m^2 m^{-2})
1990[1]	Control	394(100)[2]	—	2.46(100)
	Waterlogging	302(77)	—	1.90(77)
	SE(±)	11	—	0.88
1991	Control	323(100)	31.2(100)	1.17(100)
	Waterlogging	263(81)	20.8(67)	1.01(86)
	SE(±)	1	1.3	0.01
1992	Control	490(100)	23.3(100)	1.17(100)
	Waterlogging	363(74)	18.6(80)	0.88(75)
	SE(±)	2	0.1	0.03

1 Values in 1990 are means of three basal N treatments.

2 Figures in parentheses are percentage against control for the same year.

Table 2. Effect of N top-dressing on the crop growth rate[1] (CGR) after waterlogging.

Treatment[2]		CGR (g m^{-2} day^{-1})	
		1991	1992
Control	N0	5.79(100)[3]	3.35(100)
	N1	6.29(110)	3.55(106)
	N2	4.93(86)	
Waterlogging	N0	2.34(100)	2.49(100)
	N1	6.12(262)	4.28(172)
	N2	3.65(156)	
	SE(±)	0.95	0.98

1 Means from 1 to 40 DAW in 1991 and from 1 to 45 DAW in 1992.

2 N0, N1, and N2 represent applications of 0, 50, and 100 kg N ha^{-1}.

3 Figures in parentheses show respective CGR as a percentage of CGR without N-application for the same main treatment (control or waterlogging).

Root growth after waterlogging

Few studies have reported the effect of waterlogging on the spatial root distribution in field-grown leguminous crops (Cannell et al. 1985; Matsunaga et al. 1994). Root length density (RLD) decreased to nearly 50% of the control in both shallow and deep soil layers immediately after waterlogging (Matsunaga et al. 1994). During the subsequent recovery period the roots grew mainly in the shallow soil layers, which had been firstly noticed by Matsunaga et al. (1990) (Fig. 1). The RLD of waterlogged plants was much higher in the shallow soil layer. Promotion of adventitious roots is associated with ethylene production in tomato (Jackson et al. 1978) and maize (Drew et al. 1979). In our study, ethylene evolution of roots, shoot and soil air was measured using a gas chromatograph during or after waterlogging. However, statistically significant differences at 5% level probability were not found between control and waterlogging treatments.

Subsequent observations of root growth in our study revealed the effect of N top-dressing in more detail (Fig. 2). An increase in RLD of the waterlogged plants was restricted mainly to the shallow layer during the recovery period without N top-dressing (Fig. 2). In contrast, an Increase in RLD with N top-dressing shifted gradually from the shallow to deep soil layer during the recovery period (Fig. 2).

Soybean is reported to be more susceptible to water deficit after transient waterlogging (Sugimoto et al 1988b). Waterlogged pigeonpea may also suffer from terminal drought in October, because root development is limited in the deep soil layer. A deep root system is considered to be important in adaptation to semi-arid regions (Arihara et al. 1991). Therefore, partial recovery of the root system in the deep soil layer by N top-dressing could

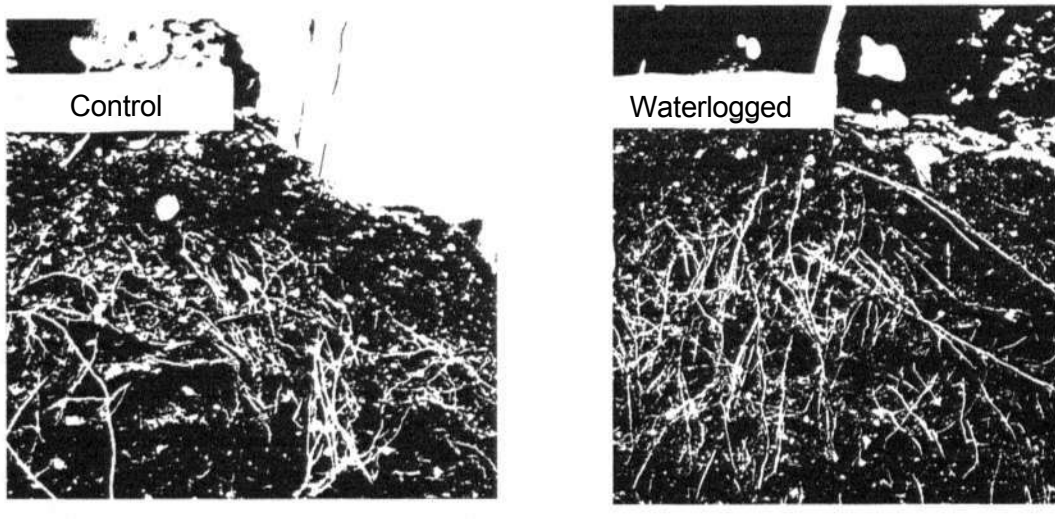

Fig. 1. Effects of waterlogging on the development of new branch roots at 40 days after the termination of waterlogging (DAW) in 1990 (From Matsunaga et al. 1992).
Photographs were taken in the plots at basal N treatment of 25kg N ha^{-1}.

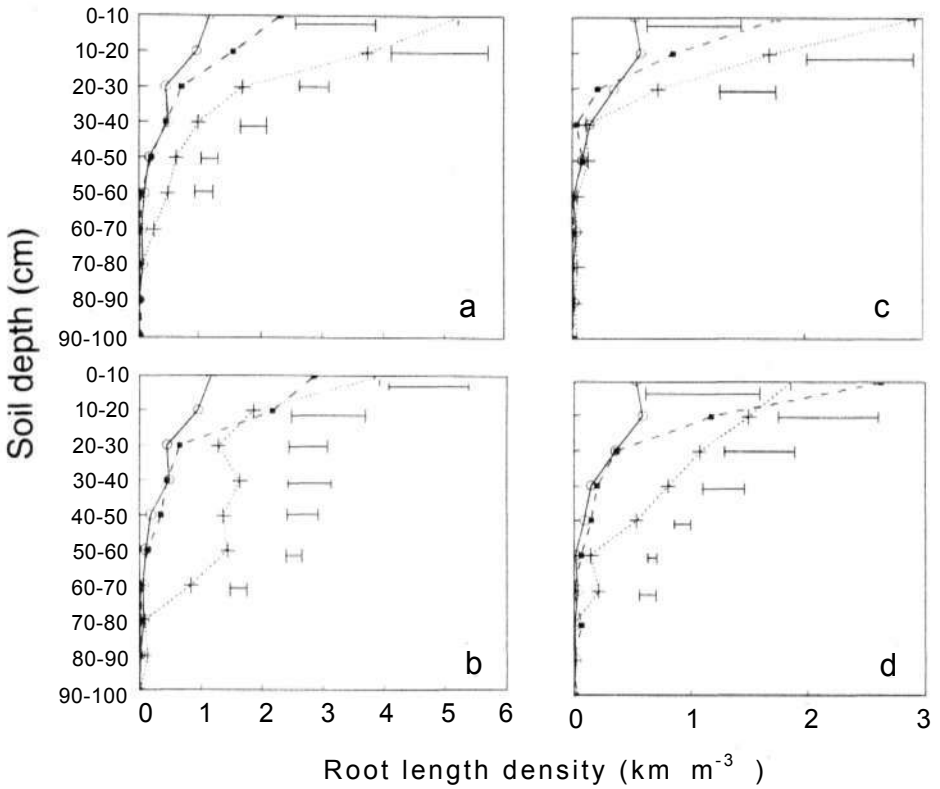

Fig. 2. Seasonal change in root length density in the different soil layers after waterlogging in 1992 (From Matsunaga et al. 1994).
Control at 0 (a) and 50 (b) kg N ha^{-1} treatments and waterlogging at 0 (c) and 50 (d) kg N ha^{-1} treatments. (—○—), 12 (---■---) and (····+····) DAW.

be important in minimizing the reduction in seed yield due to the drought after waterlogging, even though short-duration pigeonpea is infrequently subjected to terminal drought stress after the monsoon season in peninsular India (Johansen et al. 1989).

Root and nodule activity after waterlogging

Depletion of oxygen in the soil progressively reduces root growth by inhibiting aerobic respiration (Jackson et al. 1984). However, in our study, the root respiration rate recovered quickly from waterlogging damage during the subsequent recovery period, while root fresh mass of waterlogged pigeonpea stayed lower than that of the control (Fig, 3). The reduction in root fresh mass caused a reduction in total root respiration. Contrarily, N top-dressing increased root fresh mass, but decreased root respiration rate. This reduction is probably due to an increasing proportion of relatively less active parts of the roots with N top-dressing.

The processes of nodulation and N-fixation are more severely affected by waterlogging

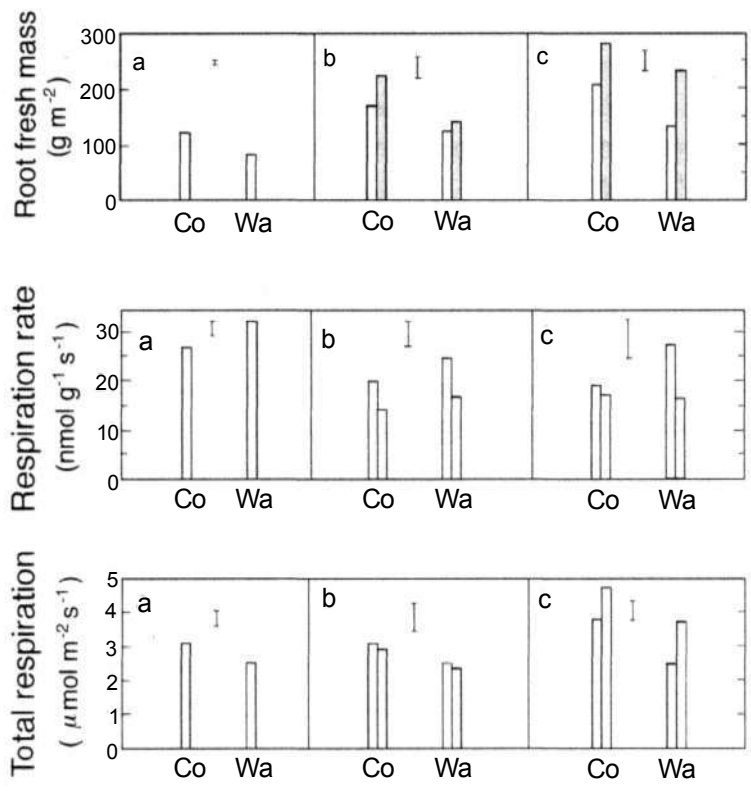

Fig. 3. Seasonal change in root respiration expressed by consumed oxygen after waterlogging. Control (Co) and Waterlogging (Wa) at 1 (a), 12 (b), and 28 DAW (c). Unshaded and shaded bars are 0 and 50 kg ha^{-1} treatments, respectively.

than any of the other plant growth processes (Smith 1987). Therefore, in our study, nodule fresh mass and specific nodule activity (SNA) were both decreased by transient waterlogging immediately after the treatment (1 DAW), resulting in considerable reduction in total nodule activity (TNA) (Fig. 4). The low SNA is probably due to low O_2 supply to the nodules at this stage (Ae and Nishi 1983; Smith 1987). However, SNA recovered quickly from the waterlogging damage, and it was higher than that in control plants. A similar increase in SNA after waterlogging was also observed for cowpea (Minchin et al. 1978). An effect of N top-dressing on TNA appeared only at 28 DAW.

The increased root respiration rate and SNA after waterlogging indicate that the root system rejuvenates during the subsequent recovery period and partially compensates for the reduction in the respiration and nodule activity caused by waterlogging. Therefore, N top-dressing contributes to the recovery of root and nodule activity by increasing the fresh mass of these components.

Alleviation of grain yield reduction caused by waterlogging

A reduction of grain yield caused by transient waterlogging has been frequently reported

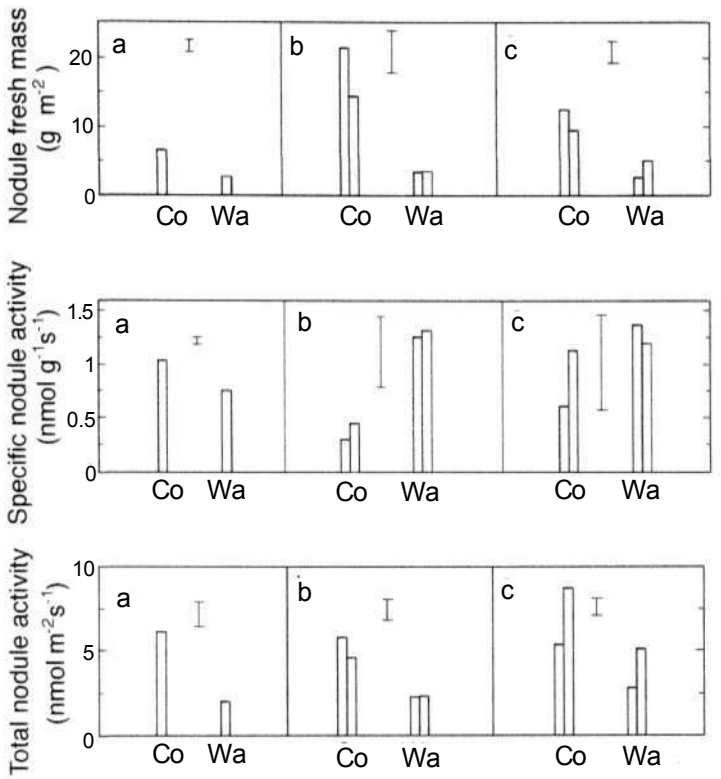

Fig. 4. Seasonal change in nodule activity expressed by evolved ethylene after waterlogging. Control (Co) and Waterlogging (Wa) at 1 (a), 12 (b), and 28 DAW (c).Unshaded and shaded bars are 0 and 50 kg ha^{-1} treatments, respectively.

for leguminous crops (Minchin and Summerfield 1976; Cannell et al. 1979; Sugimoto et al. 1988a). In our study the reduction was 35% in 1991 and 24% in 1992, as compared with the control at the NO treatment (Table 3). However, the yield difference between control and waterlogged plants became much smaller with N top-dressing due to the greater N response of waterlogged plants. The yield reduction in the N1 treatment was only 3% in 1990 and 5% in 1991, as compared with the control.

As compared with 50 kg N ha^{-1}, the application of 100 kg N ha^{-1} was less effective in alleviating waterlogging damage, due to smaller recovery of shoot and root growth, and severe depression of nodule activity in the reproductive growth stage (Matsunaga et al. 1994). It is important for maximizing seed yield to keep the nodule activity high as long as possible in leguminous crops (Lawn and Brun 1974; Troedson et al. 1989a; Troedson et al. 1989b). Consequently the dosage of top-dressing should be sufficient to increase shoot and root growth of waterlogged plants, but not so heavy as to adversely affect nodule activity. A suitable dosage as determined by this study was 50 kg N ha^{-1}.

Table 3. Effects of waterlogging and N top-dressing on grain yield (From Matsunaga et al. 1994).

N Treatment (kg N ha^{-1})	Grain yield (g m^{-2})			
	1991		1992	
	Control	Water	Control	Water
0	115(100)[1]	75(100)	112(100)	85(100)
50	122(106)	118(157)	127(113)	121(142)
100	126(110)	99(132)		
SE(±)	8		7	

1 Figures in parentheses show relative grain yields as a percentage of grain yield without N-application for the same main treatment (control or waterlogging).

Conclusion

It is important to develop new varieties of pigeonpea that can tolerate waterlogging conditions on Vertisols, because chemical fertilizer is used infrequently for upland crops in India (Burford et al. 1989). Chauhan (1987) found some genotypic differences in waterlogging tolerance in pigeonpea, suggesting the possibility of successful development of new varieties. However, this work has not been completed. Top-dressing of N to pigeonpea damaged by waterlogging proved to be reliable in alleviating the yield reduction due to waterlogging damage on Vertisols (Matsunaga et al. 1994). A deficit of N in the plants and active formation of new branch roots in the shallow soil soon after waterlogging should allow waterlogged pigeonpea to uptake applied N-fertilizer efficiently, leading to quick recovery of shoot and root growth. Therefore, N-fertilizer top-dressing should be seriously considered as an alternative technology for yield maintenance under waterlogging-prone conditions until new varieties are available.

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Root Dynamics of Cropping Systems: Major Issues and Research Needs

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Abstract

This paper summarizes the main findings of studies on root dynamics of cropping systems, focusing on root growth and activity of roots and on relations between root distribution and water uptake. Areas identified as requiring further research were understanding total plant carbon balance in relation to water and nutrient uptake, relationships between root architecture and activity (f*orm and function*)*, and the need to develop improved methodology for quantifying root function.*

Introduction

The 14 papers reviewed here cover a diverse range of topics for a variety of cropping systems. Although each paper was specific to a particular problem, in this paper 1 attempt to group the material and extract the major points that were made. I then highlight a few areas that I feel are advances in our knowledge and indicate future directions for research.

Root growth and activity

The first topic, common to several papers, was the quite detailed work on the structure and morphology of root systems, particularly of rice and other cereals (Yamauchi et al. 1996; Morita and Abe 1996). These works draw on what is an old idea, that is that through observation one can distinguish between those roots that contribute a framework and those that constitute a network capable of exploiting the soil water and nutrients. The coarse (L) and fine (S) lateral roots of rice described by Yamauchi et al. (1996) are clearly different in form (in length, diameter, and vascular anatomy), raising the question as to whether or not their function also differs. The S roots make up the majority of the root length in young rice plants and so are likely to be important in the uptake of nutrients. Their length and structure are visually similar to the ephemeral roots shown in the mini-rhizotron pictures of

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Huck at this workshop, thus perhaps the "network" roots are short-lived and senesce when their mining function has been fulfilled. Although these are interesting observations, there is a need for critical experiments that will assess the physiological differences between root types.

During this workshop, there were several descriptions of the overall patterns of root growth as deduced from field experiments (Lee et al. 1996; Ito et al. 1996; Krishnamurthy et al. 1996). These works are subject to a number of criticisms in terms of the methodology used and each researcher pointed out the difficulties that they had encountered in interpreting their data. The principal limitation to much of the current methodology is that it gives the balance between growth and decay, i.e., the net production. This is also what is measured when shoot growth is assessed by agronomists. For example, a plant of wheat grown in a stand typically produces about 12 leaves and 4 or 5 tillers yet at maturity probably only about 5 or 6 leaves and 1 or 2 tillers are still visible, the remainder having died and decomposed during the growing season. Such considerations do not prevent physiologists and agronomists using shoot weight as an indicator of production so that, even with their limitations, the patterns of root growth described are useful for indicating the overall distribution of resources within the plant.

The descriptions of how roots are distributed within the soil profile show differences between workers and indicate the dynamic nature of the root/soil system. Gregory (1996) and Krishnamurthy et al. (1996) presented data showing that the distribution of roots within the soil profile could be described reasonably well by an exponential function during vegetative growth (Greenwood et al. 1982). However, this is by no means universally applicable (e.g., Lee et al. 1996) and both non-uniformities within the soil profile (e.g., zones of nutrient accumulation or of physical impedance) and the senescence of roots will affect the distribution in both the short and long term. Typically most profiles contain most nutrients at the top (A horizons are typically thinner and more nutrient-rich than B horizons), but in soils where nutrients are mixed throughout the profile (e.g., many vertisols) or leached to depth by heavy rainfall, then the root distribution may reflect this altered distribution of nutrients.

Throughout this workshop, there was a general concern that plants should be regarded as whole organisms and that the mechanisms for the maintenance of root:shoot homeostasis should be appreciated. Again, this is a subject whose importance has been recognized for many years and the idea of a functional equilibrium between roots and shoots has proved useful in understanding the observed responses of roots and shoots to their environments, and the partitioning of dry matter between them (van Noordwijk and de Willigen 1987). Although Davidson (1969) expressed the relation between aerial and underground parts in terms of the mass and activity of both components, the difficulty in quantitatively defining the activity still exists. For shoot systems, the principal activity is the interception of radiation and its conversion to dry matter. Considerable progress has been made in developing robust methods of expressing these terms. Dry matter production can now be expressed quantitatively (if water, nutrients, and diseases are not limiting factors) as the product of the incident radiation, the fraction of radiation intercepted (a function of leaf area index), and the conversion coefficient of radiation to dry matter (a conservative quantity). For root systems the activities required are more diverse than those

of shoots, and the resources to be acquired by them are sometimes low in concentration and diffuse. For example, nutrient ions are not uniformly distributed with depth and it is still difficult to define the instantaneous availability of any particular nutrient (Hunt et al. 1990).

Roots and water uptake

The work of the Japanese group at ICRISAT has examined below-ground interactions in detail at particular sites and seasons. There is a need to generalize the findings so that they can be applied to other seasons and soils.

Two results may indicate the emergence of useful relations between the amount of root present and the activity of the root system in extracting water.

First, the paper of Payne et al. (1996) presented results of a 2-year study in Niger on the effects of phosphorus (P) application on growth and water use by three genotypes of pearl millet including a landrace. Even in water-limited environments, nutrients are limiting so that responses to fertilizer are common. Although root growth was similar between genotypes, the landrace tended to produce more roots in deeper soil layers (>0.4 m) particularly when P-fertilizer was applied. Such increases in root length may be advantageous for soil water extraction during dry periods or at times of high water demand.

Second, Krishnamurthy et al. (1996) examined the patterns of root growth of chickpea varieties in relation to water extraction and drought tolerance. There was large genotypic variation in the extent of root proliferation related to the rate of soil water depletion. In their comparison of two varieties, ICC 4958 and Annigeri had similar total root length (ICC 4958 was slightly longer in one season) and rooting depth in two consecutive years when grown on a vertisol. However, the distribution of roots was different: ICC 4958 had greater root length densities in deeper layers for much of the season. There was a linear relationship between the rate of water extraction from moist soil layers and the root length density up to the maximum root length recorded (0.4 cm root cm'^{3} soil). Other trials had previously shown ICC 4958 to be drought tolerant over a range of semi-arid environments, and the work by Krishnamurthy et al. (1996) indicates that this genotype is able to extract significantly more water from the surface soil layers (to 30 cm) early in the season. The timing of water use and the production of a more prolific root system to depth appear to be associated with the drought tolerance of ICC 4958.

Future research

Biologists are generally very good at measuring the rates of various processes, but less attentive at specifying their duration. This general issue will require attention if progress is to be made in quantifying root performance. It is quite clear that if crops are growing on a limited supply of soil water and one crop uses the water at a faster rate than the other, then the rate will be maintained for a shorter period. So, rates and durations are almost

invariably inversely related. It is important to define the duration for which a process must be maintained before deciding whether a higher rate would be beneficial.

This review highlights three areas for research. First, the carbon balance of the plant is an issue in relation to both nutrient and water acquisition by crops and to sources and sinks of carbon globally. To answer such questions as "how much material is lost by sloughing of root cells and exudates" and "what is the seasonal C turnover of root systems" will require the development of new techniques. The current pulse labeling procedures have the limitations because the label is concentrated in the more labile components of the root system. The development of continuous labeling techniques would open up possibilities of measuring both rates and durations of processes. A link needs to be made with the current fad for estimating root turnover using mini-rhizotron techniques. Although root turnover is observed, does it actually lead to much loss of carbon, nitrogen, or other nutrients? Or, as when leaves senesce, are many of the materials translocated to other active parts and so re-used?

The second area for research is that of form and function. We observe different types of roots, but is there any physiological reason for assuming that small, thin roots are able to take up nutrients and large, fat ones are not? It may well be, of course, that short-lived roots with minimal investment in structural materials do extract the most readily available nutrients and that because there are so many of them they do, in fact, take up the majority of the nutrients. However, it is worth reflecting on the whole area again and determining whether the inferences drawn from observation are realized in practice.

A related question is, in what circumstances are water and nutrient uptakes limited by the size and distribution of the root system? The relation between rate of water extraction and root length density determined by Krishnamurthy et al. (1996) fits quite well with the theoretical calculations made by Passioura (1982) and de Willigen and van Noordwijk (1987) on the amount of root length beyond which one would not expect to obtain an increased rate of water uptake (typically 0.5 to 1.0 cm root cm"^{3} soil). Similar measurements are required for less mobile nutrients in soils relevant to semi-arid conditions.

Both of these research areas relate to that of architectural complementarity referred to by several researchers in this workshop. Temporal complementarity is easy to comprehend in such systems as sorghum/pigeonpea intercropping in which sorghum is present for only a small part of the total cropping cycle; but can spatial complementarity increase the production of cropping systems?

The final area for research is that of methodology. Present methods of measuring root growth and function are crude. Furthermore there was much discussion during the workshop about the non-standardization of techniques between researchers; for example, the variability that can result because of the use of different mesh sizes when washing roots from soil. New techniques are being developed and the introduction of non-destructive methods, such as computer-assisted tomography with either gamma-or x-ray sources (Aylmore 1993), and nuclear magnetic resonance techniques (Crestana et al. 1985), will allow rates and durations of various processes to be obtained. These are obviously not field techniques, but when combined with isotopic and continuous labeling techniques will open up the possibilities of exploring root/soil interactions of relevance to cropping systems.

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Differences in Carbon and Nitrogen Utilization Between Cereals and Legumes

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Abstract

Two models for carbon-nitrogen (C-N) interaction were developed: one, expressed as $DM = DM_0 \times Exp(CNI \times N_t)$, *was for the growth of cereals (rice, winter wheat, spring wheat, and maize), and the other,* $DM = DM_0 + CM' \times N_t$, *for legumes (soybean, field bean, and adzuki bean); where DM is the dry weight of a plant at a given time,* N_t *is the amount of N accumulated in the plant at a given time,* DM_0 *is the initial dry weight, and CNI and* CM' *are the C-N indices. The CNI value changed with the amount of N accumulated at the time of harvest (*N_h*), indicating that the relationship between the CNI value and* N_h *fitted to a hyperbolic curve is* $CNI = 1/(aN_h + b)$, *where a and b are the coefficients of the equation. The CNI' value of legumes was almost constant regardless of* N_h.

The low productivity per unit amount of N accumulated in legumes compared with that in cereals during the vegetative growth stage was caused by the low growth efficiencies [*accumulated dry matter/*(*accumulated dry matter + respiration*)] *of whole plants. This efficiency was related to the high* ^{14}C *allocation ratio of* ^{14}C *compounds assimilated into organic acids and amino acids in leaves irrespective of N nutrition.*

In cereals, P-N, K-N, and Mg-N relationships during growth were $P = P_0 \times Exp(PNI \times N_t)$, $K = Kmax/(1 + KM \times (DM_0 \times Exp(CNI \times N_t))^{-1})$, *and* $Mg = Mg_0 + MgNI \times N_t$, *respectively. In legumes, they were* $P = P_0 + PNV \times N_t$, $K = K_0 + KM' \times N_t$, *and* $Mg = Mg_0 + MgNI' \times N_t$, *respectively, where* P_0 *and* Mg_0 *are initial values, and CNI, PNI, Kmax, KNI, MgNI,* CM', *PNV, KNI', and MgNI' are coefficients. Thus, mineral accumulation models in relation to* N-*accumulation in legumes were quite different than those in cereals. This difference suggests that because P and K nutrients are related intimately to C and N metabolism, the difference in the P-N and K-N accumulation models between cereals and legumes is presumably caused by the difference in C and N metabolism between cereals and legumes. On the other hand, Ca and Mg are not strongly related to the balance in C and N metabolism.*

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Introduction

Ingestad (1977) reported that the relative growth rate (RGR) had a close correlation with nitrogen (N) content of tree seedlings. This concept has been widely used in developing models of RGR as a function of N-content of whole plants (Hirose 1988; Pons et al. 1994). However, in field crops, it has been difficult to directly relate RGR to N-content: Greenwood et al. (1991) developed a model that relates a modified RGR to N-content.

In his classic study, Blackman (1919) reported that the amount of dry matter of a plant increases exponentially with time, consistent with the concept of dry matter accumulation rate (plant photosynthetic rate) being catalyzed by the amount of plant dry matter. This is expressed by the equation

$$DM = DM_0 \times Exp(RGR \times t), \quad (1)$$

where DM is the dry weight of the plant, DM_0, is the initial dry weight, RGR is the relative growth rate, and t is time. Although this model fits well for the early stages of plant growth, it dose not fit well for later growth. Assuming that plant growth is strictly regulated by N-nutrition, based on Blackman's concept, it is possible to develop a carbon-nitrogen (C-N) interaction model for growth as

$$DM = DM_0 \times Exp(CNI \times N_t), \quad (2a)$$

where N_t is the amount of N accumulated in the plant at a given time and CNI is the carbon-nitrogen index (Osaki et al. 1992). Osaki et al. (1992) found that the C-N balance of cereals (rice, wheat, and maize) agreed well with above equation, whereas that of legumes did not. However, the C-N balance of legumes corresponded closely with the model represented as

$$DM = DM_0 + CNF \times N_t, \quad (2b)$$

where the CNF is the C-N index of legumes. Lemaire et al. (1992) found that this same model is applicable to lucerne (*Medicago sativa* L.).

To explain this difference in productivity per unit of N absorbed between cereals and legumes, Tanaka and Yamaguchi (1968) used growth efficiency (GE), estimated as AW/(AW + R), where AW is the increment in dry matter production and R is the amount of respired substrate. On the other hand, on the basis of information on biochemical pathways and energetics, Penning de Vries et al. (1974) and Penning de Vries (1975) estimated the efficiency of dry matter production (i.e., production value, PV), which is defined as the amount of a certain compound synthesized from a unit amount of substrate required for carbon skeletons and energy production. In general, low productivity of soybean is due to its high content of protein and lipid in seeds (Sinclair and de Wit 1975). Shinano et al. (1993) compared experimentally obtained GE and theoretically calculated PV for dry matter of harvested organs of 20 field-grown crops. The GE of harvested organs was generally higher than the PV for dry matter, especially in legumes. Shinano et al. concluded that low

productivity of legumes can not be attributed to the high respiratory loss of carbohydrates in harvested organs. Tanaka and Osaki (1983) fed $^{14}CO_2$ to whole plants of rice, wheat, maize, soybean, and field bean, and then determined the release of $^{14}CO_2$ from the plant. They observed more $^{14}CO_2$ released from soybean and field bean than from rice, wheat, and maize. Though Shinano et al. (1991) assumed that this high rate of $^{14}CO_2$ release from legumes was due to consumption of current photosynthates by respiration, they found that soybean also respired a larger amount of $^{14}CO_2$ from storage substances than did rice. These results suggest that legumes consume more current photosynthates and/or temporary storage substances for respiration in leaves and stems than do cereals. In this paper, we discuss further the difference in C-balance and allocation of ^{14}C compounds between cereals and legumes.

The balance of C and N metabolism is different between cereals and legumes. Because phosphorous (P) and potassium (K) are important nutrients for photosynthesis, respiration, energetic metabolism, and C and N metabolism, we need to know how P and K affect the C-N interaction. Phosphorus is an important nutrient for C and N metabolism in that (a) under P-deficiency conditions, nitrate absorption and nitrate reduction are suppressed before retardation of protein synthesis (Rufty et al. 1990; Schjorring 1986); (b) accumulation of phosphate decreases and translocation increases in maize; (c) under P-deficiency, PEPC and PEP phosphatase activity increases, causing triose-phosphate to dominate and to distribute into amino acid metabolism through the tricarboxylic acid (TCA) cycle (Duff et al. 1989; Theodorou et al. 1990; Theodorou and Plaxton 1993); (d) photosynthetic rate relates to P-nutrition, as well as N nutrition (Tanaka and Hara 1971); (e) starch accumulation in grains of cereal crops accompanies P accumulation in grains (Shinano et al. 1990); and (f) root/shoot ratio are affected by the N/P supply ratio (Adalsteinsson and Jensen 1988). Potassium is also an important nutrient for C and N metabolism in that (a) K-nutrients contribute in the stabilization of enzyme activity; (b) soluble N-compounds increase with K-deficiency (Tanaka and Hara 1972; Mengel and Helal 1968); (c) respiratory rate increases with K-deficiency (Tanaka and Hara 1972; Peoples and Koch 1979); and (d) both phloem loading and transport of sucrose are enhanced by K (Mengel and Haeder 1977; Doman and Geiger 1979). Thus, we hypothesized that mineral (P, K, Ca, and Mg) accumulation, especially that of P and K, will be different between cereals and legumes because the C-N balance is quite different between cereals and legumes. To assess this hypothesis, we examined mineral accumulation in relation to N-accumulation during growth under field conditions.

The relationship between C and N

Relationship throughout plant growth

Figure 1 shows relationships between the amount of DM and N during growth in cereals (rice, winter wheat, spring wheat, and maize) and legumes (soybean, field bean, and adzuki bean). Data for each crop were collected from field experiments where high yields

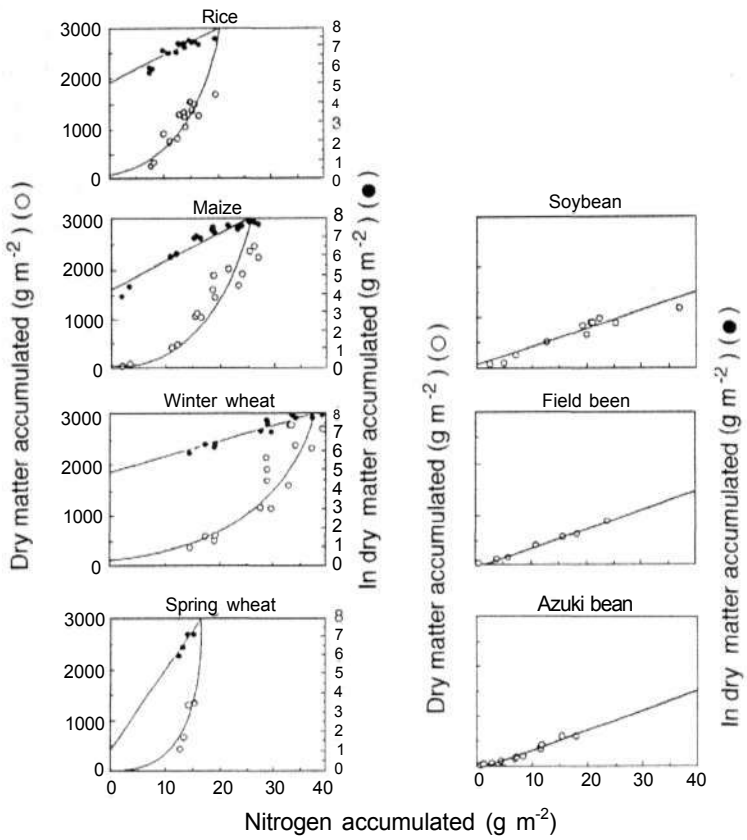


Fig. 1. Relationship between dry matter and N-accumulation during the growth in high yielding varieties of cereals and legumes (modified from Osaki et al. 1992).

were obtained (Osaki et al. 1992). As the amount of DM increased exponentially with the increase of N in cereals, the DM-N relationship for these crops fitted well to Equation (2a) (significant at the 5% level). However, because the amount of DM increased linearly with increase in N in legumes, the DM-N relationship of three legumes fitted better to Equation (2b), which was significant at the 5% level, than to Equation (2a). For cereals, the CNI value of high-yielding varieties was the lowest in winter wheat (0.08), highest in spring wheat (0.42), and intermediate in other crops (0.10 to 0.19) in cereals. For legumes, the CNF value of high-yielding varieties varied only slightly, from 34 to 35.

Relationship at harvest

The DM-N relationship of various crops at harvest was examined. The dry matter at harvest (DM_h) showed a close relation with the amount of N accumulated at the time of harvest (N_h) (data not shown). The relationship was hyperbolic for rice, winter wheat, and maize, but linear for soybean. To model the DM_h-N_h relationship, we used the scheme illustrated in Figure 2a for the relationship between DM or DM_h and N or N_h. According to this figure, when a small amount of N is applied, the CNI value is likely to increase. However, because N_h decreases, DM_h is also low. If a large amount of N is applied, the CNI

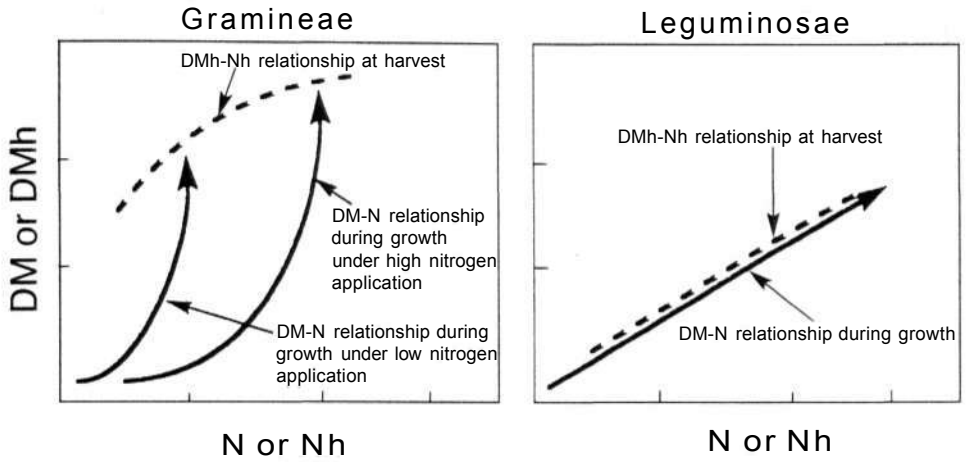


Fig. 2. Scheme of DM-N relationship at harvest and during growth in cereals and legumes (after Osaki et al. 1992).

value is likely to be low. However, because N_h increases, DM_h increases. Thus, we assumed that there is also a close relationship between the CNI value and N_h or DM_h. Assuming the relationship between the CNI value and N_h is represented by a hyperbolic curve, then

$$CNI = 1/(a \times N_h + b) \quad (3a)$$

where a and b are constants estimated by regression using the data of CNI and N_h if there is a data set of DM and N at the successive growth stages at each treatment.

For low a and b values, the productivity per unit amount of N absorbed was high because the CNI value was increased (Fig. 3). Photosynthetic rate strongly correlated with leaf N-content based on leaf area, and photosynthetic rates of C_4 plants to unit N-content was 2~3 times higher than that of C_3 plants (Sinclair and Horie 1989). Therefore, C_4 plants are assumed to have a higher value of N-use efficiency than C_3 plants (Brown 1978). Figure 3 shows that the a and b values of maize (C_4 plant) was higher and lower, respectively, than that of rice (C_3 plant), causing the productivity per unit amount of N absorbed in maize to be higher at small N_h than in rice, whereas it was the same at high N_h (around 20 gN m^{-2}) as compared with rice. Thus, the difference in productivity per unit amount of N absorbed between rice and maize changed according to the N-nutrient levels. The relationship between photosynthetic rate and N-content in the leaf was not, therefore, an indicator of N-use efficiency of the whole plant.

In legumes, because the relationship between DM_h and N_h was linear, and the DM_h-N_h relation was similar to the DM-N relation, the DM_h-N_h relation can be expressed as

$$DM_{,,} = DM_0 + CNT \times N_h \quad (3b)$$

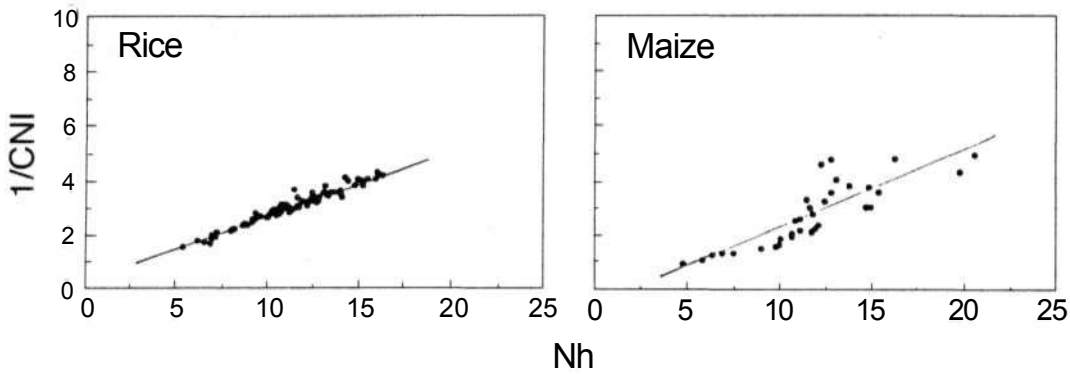


Fig. 3. Relationship between 1/CNI and N-accumulation at the time of harvest (N_h) of rice and maize. Both crops were grown with different rates of fertilizer application (modified from Osaki et al. 1996).

Yamaguchi and Tanaka (1981) ascribed this basic difference between cereal and legume crops the larger amounts of energy respired during N_2 fixation in root nodules. To test this hypothesis, we examined the DM-N relationship in isogenic lines [A62-1 (nodulated) and A62-2 (non-nodulated)] of soybean. The effect of nodulation or N_2 fixation on the DM-N relationship is almost negligible (Osaki et al. 1992), indicating that the respiratory loss of carbohydrates for N_2 fixation is not large enough to significantly change the DM-N relationship in soybean.

Growth efficiency and ^{14}C distribution

Growth efficiency

The growth efficiency (GE) is calculated as the GE(DW) from the data of dry weight and the amount of respired CO_2 (as CH_2O) of the whole plant at vegetative stages. The GE(DW) is about 0.10 higher in rice than in soybean (Shinano et al. 1995), and slightly lower at high N application regardless of crops or experiments. This explains the lower productivity in soybean than in rice (Fig. 4). Because the temperature in 1991 was lower than in 1993, we expected the growth efficiency to be higher in 1991 due to maintenance respiration being depressed by low temperature. However, the effect of temperature on growth efficiency was negligible. One function of maintenance respiration is assumed to be protein turn-over (Penning de Vries et al. 1974). Nevertheless, we found that protein content (variation within 22 to 33%) in leaves had only a slight effect on GE in both crops. Thus, maintenance respiration dose not explain the difference in productivity between cereals and legumes.

The composition of chemical components can be divided into crude protein, crude lipid, and crude carbohydrate, which have a C-content of 55.8, 76.9, and 42.0%, respectively

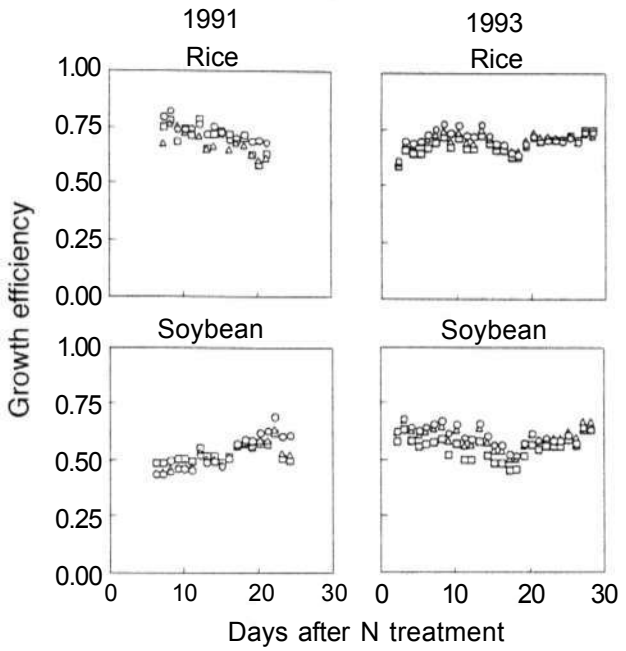


Fig. 4. Changes in growth efficiency of whole plant during growth in 1991 and 1993. Seeds of rice and soybean were sown on vermiculite in a greenhouse on 8 Aug and 6 Sep in 1991, respectively, and 1 and 18 May in "1993, respectively. Temperature during growth was higher in 1993. Plants were grown by hydroponic culture for three different N levels. Here, ○ is 5 ppmN (5N in 1993); △, 30 ppmN (15N in 1993); □, 90 ppmN (30N in 1993) (after Shinano et al. 1995).

(Shinano et al. 1993). To determine the effect of the difference of C-content on GE, we calculated the GE based on C-content (GE(C)). Though the GE(C) was approximately 0.10 to 0.15 higher than the GE(DW), the GE(C) of soybean was still lower than that of rice.

Vertregt and Penning de Vries (1987) calculated the production efficiency (PV) of synthesizing protein, lipid, and carbohydrate by using 1g glucose according to biochemical pathways the PV was 0.56, 0.33 and 0.81, respectively. By using these efficiencies and the content of each chemical component, we also calculate the GE(PV) as GE(PV) = 100/(protein%/0.56 + lipid%/0.33 + carbohydrate%/0.81). Though the protein content of the leaves of soybean in 1993 was about 10% higher than that of rice, the calculated GE(PV) was also similar among crops. Thus, the difference of 0.10 to 0.15 in experimentally obtained GE(DW) between rice and soybean can not be explained by the efficiency of synthesizing each chemical component.

It is generally agreed that the difference in productivity between cereals and legumes is explained either by their difference in protein content (Yamaguchi 1978) or by their difference in biochemical efficiency of the energy requirement for protein synthesis (Penning de Vries et al. 1974) and maintenance (protein turn-over) (Penning de Vries 1975). However, our results indicate that chemical components were quite similar among cereals and legumes during the vegetative growth stage and, moreover, the effect of the N-content and temperature on the GE was negligible. This confirms that different respiratory mechanisms of leaves or whole plants between cereals and legumes cannot be accounted

for by a concept of growth or maintenance respiration.

^{14}C distribution

A large portion of N-compounds in sink organs is accumulated in leaves and stems and then decomposed and translocated to the sink organs in rice and soybean (Osaki et al. 1991) as follows; [protein in leaves] —> [free amino acids in leaves] —>[free amino acids in stems] —> [free amino acids in sink organs] —> [protein in sink organs]. We calculated the changes in C/N ratio in each component in the scheme of rice and soybean at the mid-ripening stage by using the data of Osaki et al. (1991). The C/N ratio did not change significantly among each component in rice (between 3.0 to 3.4). On the other hand, the C/N ratio in soybean decreased remarkably between free amino acids in leaves (3.1) and those in stems (1.9), then increased again between free amino acids in sink organs (2.7) and those in protein of sink organs (3.0). This difference may be caused by formation of asparagine, which is the major translocating compound of N in soybean (Osaki et al. 1991). However, the respiratory loss of ^{14}C from ^{14}C-[U]-sucrose and ^{14}C-[U]-asparagine introduced to the source leaves was not significantly larger in leaves of soybean (26~33% and 21~23%, respectively) than in leaves of rice (23~33% and 26-30%, respectively). These results show that changes in the C/N ratio in the process of translocating the amino acids were not large enough to explain the high respiratory rate in the leaves and stems of soybean.

In contrast to ^{14}C-sucrose and ^{14}C-asparagine, the behavior of photosynthesized $^{14}CO_2$ is quite different between rice and soybean (Shinano et al. 1994). In soybean, a large amount of photosynthesized $^{14}CO_2$ is respired under light compared with that under dark, but the amount of ^{14}C retained in the leaves is similar regardless of light conditions in rice (Fig. 5). This high respiratory loss of current photosynthate in soybean under light conditions can be explained partly by its high photorespiratory rate in the leaf, because $^{14}CO_2$ release from the $^{14}CO_2$ assimilated leaf of soybean gradually decreases with time compared with that of rice (Fig. 5). In addition, after the first high $^{14}CO_2$ release (presumably photorespiration) from the $^{14}CO_2$ assimilated leaf of soybean, $^{14}CO_2$ release remains high, compared with that of rice. This indicates that not only photorespiratory activity, but also TCA cycle activity or another metabolic activity of amino acids and organic acids remains high for a long time in soybean. Shinano et al. (1994) also demonstrated that under dark conditions, as $^{14}CO_2$ release from $^{14}CO_2$ assimilated in leaves of soybean is higher than that of rice (Fig. 5), the activity of the TCA cycle is maintained high in the dark. Champigny and Foyer (1992) proposed a hypothesis that the distribution of photosynthetically fixed C to sucrose and amino acids is mainly regulated by the activity of sucrose phosphate synthase (SPS) and phosphoenolpyruvate carboxylase (PEPC), respectively, which depend on light and nitrate conditions. In our experiments, we found that a large portion of photosynthetically fixed $^{14}CO_2$ in soybean under light conditions was distributed to organic acids, amino acids, and protein compared with that in rice (Fig. 6). In soybean, ^{14}C distribution to organic acids, amino acids and protein from $^{14}CO_2$ increased in the source leaf with N-application; but this was not the case in rice (Fig. 6). Therefore, according to the hypothesis of Campigny and Foyer (1992), the PEPC activity is relatively higher than the SPS activity in soybean compared with rice. When N-appiication is stopped

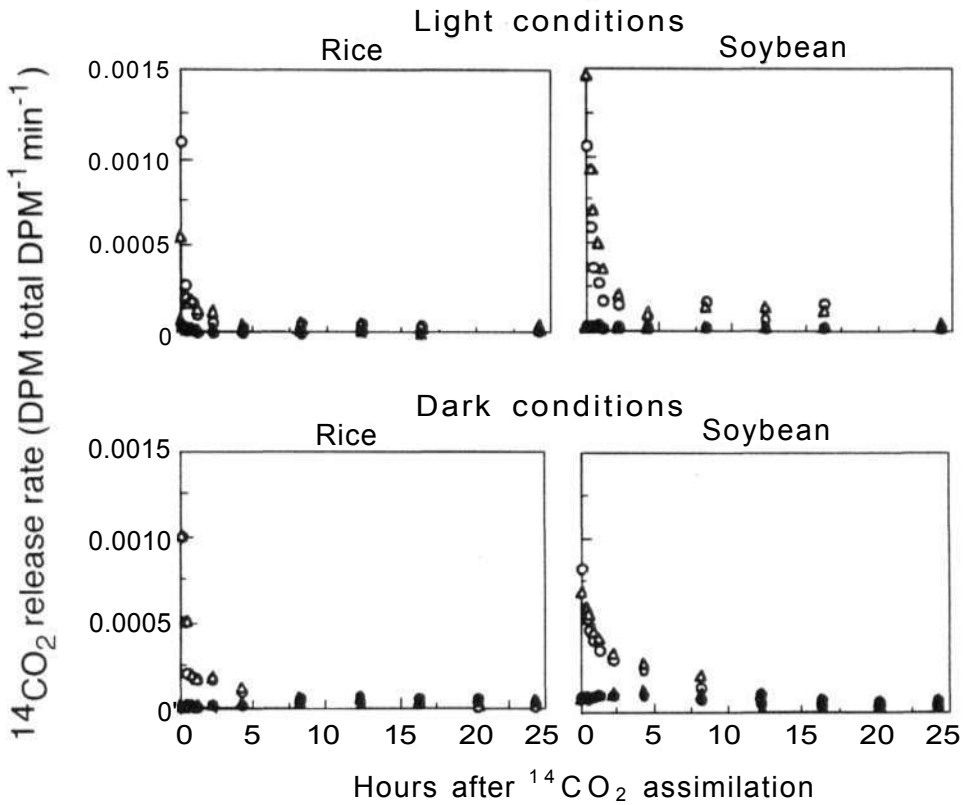


Fig. 5. $^{14}CO_2$ release rates from the leaf and sink organs after $^{14}CO_2$ assimilation. Here, ○ is ON-source leaf; ●, 0N-sink organ; △, 60N-source leaf; ▲, 60N-sink organ (after Shinano et al. 1994).

at 0N, leaf N content is severely decreased in soybean (Shinano et al. 1994). Nevertheless, we found that the distribution ratio of photosynthetically fixed C into N compounds was still high compared with that in rice at 60N (Fig. 6). Therefore, the difference between the mechanism for the distribution of photosynthetically fixed C into nitrogenous and organic compounds in rice and soybean was basically unchanged by N-status.

Mineral accumulation in relation to N-accumulation

Because we found that C-N interaction was quite different between cereals and legumes, we assumed that the accumulation of other minerals, such as phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), also is assumed to be different between cereals and legumes due to the effect of those minerals on C and N metabolism. Accumulation of each of these minerals is thus related to N-accumulation because N is the most important nutrient.

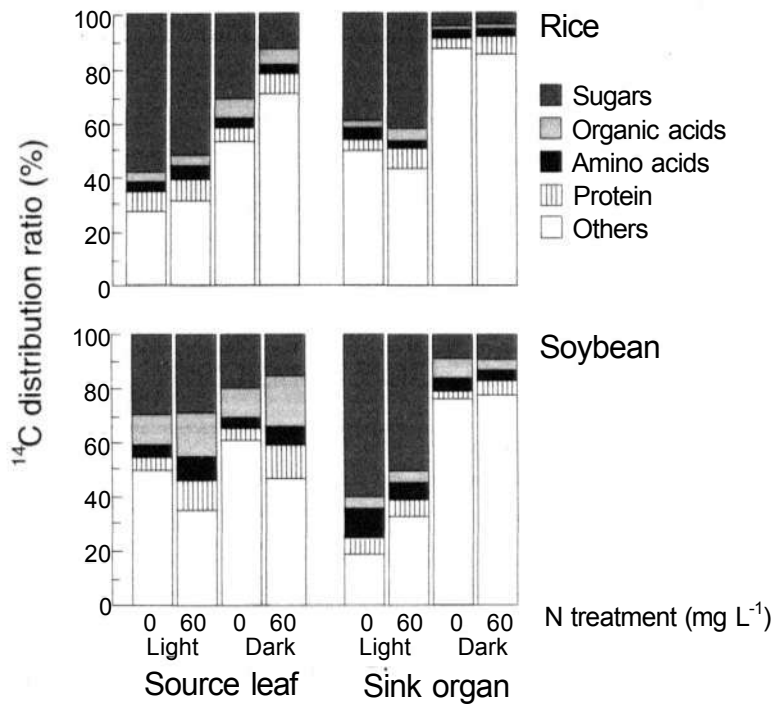


Fig. 6. ^{14}C distribution into each chemical component in the source leaf and the sink organs after $^{14}CO_2$ assimilation (30 min.) (after Shinano et al. 1994). Plants ^{14}C-assimilated were set in each light condition, then were sampled at 24 hours after $^{14}CO_2$ assimilation.

Phosphorus

In cereals, the amount of P-accumulation (P_t) increased exponentially with the increase in N_t, like the DM-N interaction (Fig. 7). Osaki et al. (1996) developed P-N interaction model for growth as follows

$$P_t = P_0 \times Exp(PNI \times N_t), \quad (4a)$$

where P_0 is the initial P_t, and the PNI is the P-N index. In legumes (soybean and field bean), the model becomes

$$P_t = P_0 + PNI' \times N_t, \quad (4b)$$

where the PNI' is the P-N index for legumes.

Note that the values for the CNI and PNI are positively correlated and relate to each other as (Fig. 8)

$$PNI = cCNI + d, \quad (5)$$

where c and d are constants. This strong correlation suggests that C, N, and P are

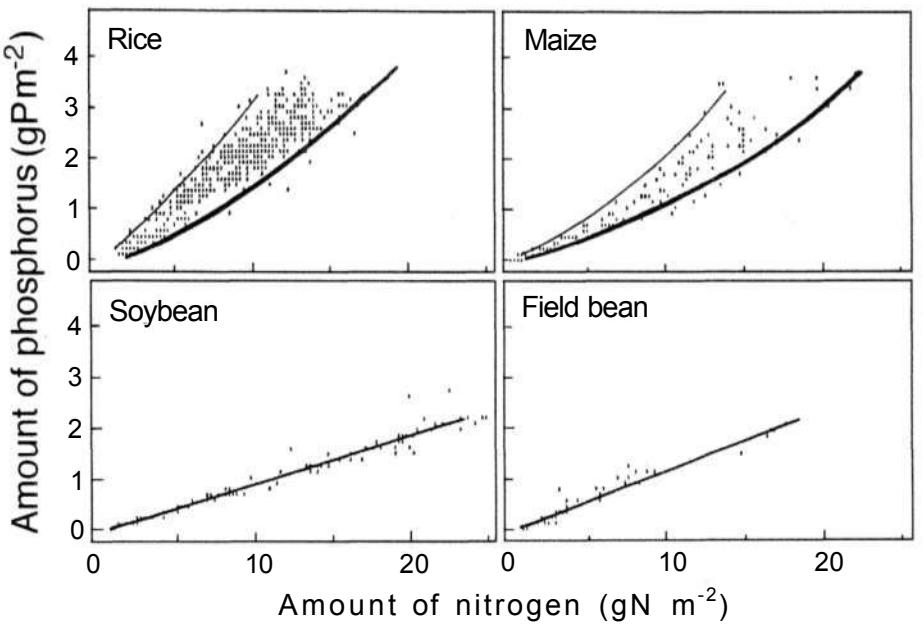


Fig. 7. Relationship between amount of P and amount of N accumulated at successive growth stages. Crops were grown with different rates of fertilizer application (modified from Osaki et al. 1996). In cereals, ——— is a typical case of high PNI, ——— is a typical case of low PNI. In legumes, ——— is a regression that includes all treatments.

accumulated under mutual interaction. When the N-application rate is small, the CNI is high, and when P-application rate is small, the PNI is low. As P is required for starch accumulation, C-metabolism for starch synthesis is depressed under low P nutrition, especially during ripening. Theodorou and Plaxton (1993) reported that a considerable induction of PEP phosphatase and PEPC occurred when suspension-cell cultures were transferred to media that lacked inorganic P, suggesting that through the induction of alternative pathways of glycolysis and mitocondrial electron transport, sucrose is consumed by the TCA cycle or is distributed to amino acids. According to the concept of Champigny and Foyer (1992), when the PEPC activity increases under P-nutrition, photosynthetic C is diverted to organic acids or amino acids. Therefore, the C-N interaction will change according to P-nutrition as shown in Figure 8.

Potassium

In cereals, the relationship between amount of K absorbed (K_t) and N_t is expressed as a sigmoid curve (Fig. 9). Therefore, the K-DM interaction model is

$$K_t = Kmax/(1 + KNI \times DM,, \times Exp(CNI \times Nt)^{-1}) \quad (6a)$$

where Kmax and KNI are constants (Osaki et al. 1996). In Equation (6a), the relationship between Kmax and KNI is expressed as a regression significant at the 1 % possibility level

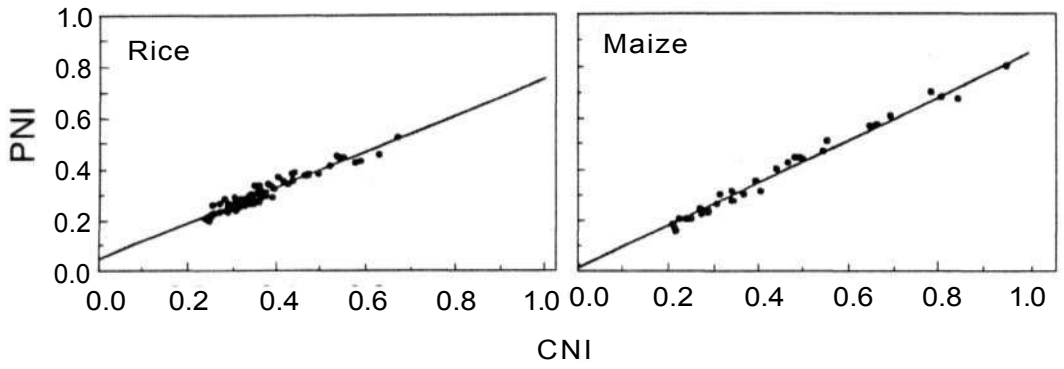


Fig. 8. Relationship between PNI and CNI for rice and maize (after Osaki et al. 1996)

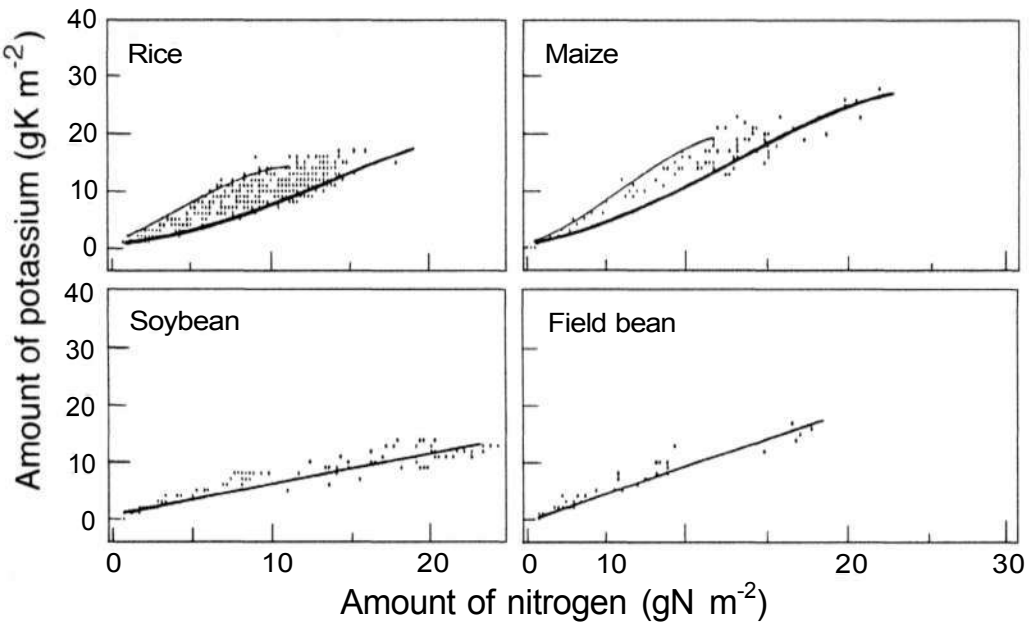


Fig. 9. Relationship between amount of K and amount of N accumulated at successive growth stages. Crops were grown with different rates of fertilizer application (modified from Osaki et al. 1996). In cereals, —— is a typical case of low KNI, ▬▬ is a typical case of high KNI. In legumes, —— is a regression that includes all treatments.

$$Kmax = e \times KNI + f \quad (7)$$

where e and f are constants. The relationship between CNI and KNI is not clear, whereas, KNI tends to increase with the decrease in CNI (Fig. 11).

In legumes, the K-N model is

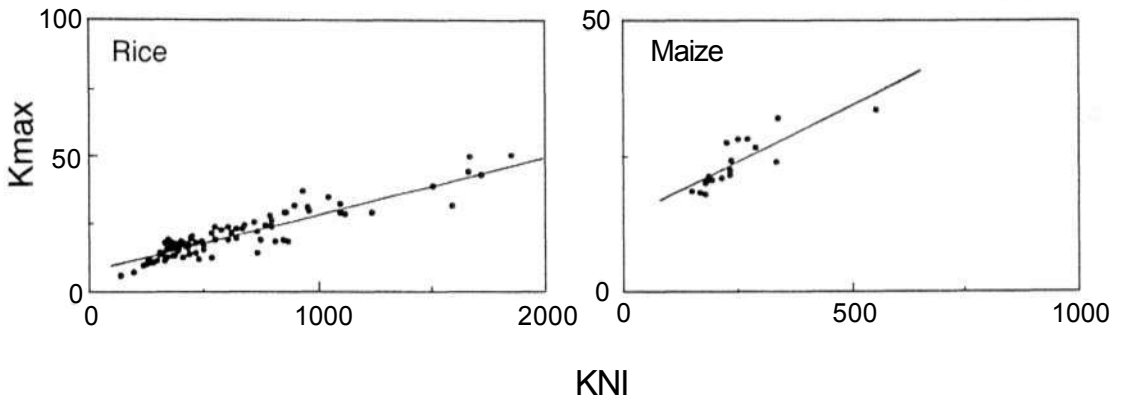


Fig. 10. Relationship between Kmax and KN1 for rice and maize (after Osaki et al. 1996)

$$K_t = K_0 + KM' \times N_{t'} \quad (6b)$$

where K_0 is initial K, and KNF is the K-N index.

Calcium

Because the relationship between N_t and the amount of Ca accumulated are not consistent among crops (Fig. 12), it is difficult to develop a general Ca-N interaction model (Osaki et al 1996). Compared with the Ca-N relationship in cereals, that in legumes changes according to growth stage. This tendency did not improve even if Ca correlated to DM.

Magnesium

In all crops, including legumes, the amount of Mg accumulated (Mg_t) increases linearly with an increase in N_t (Fig. 13), and the Mg-N model is linear at 1% probability level as (Osaki et al. 1996)

$$Mg_t = Mg_0 + MgNI \times N_t \quad (8)$$

where Mg_0 is initial Mg_t, and the MgNI (MgNF in the case of legumes) is the Mg-N index. The Mg accumulation appear to be strictly regulated by N-absorption in both cereals and legumes.

Conclusion

Productivity in relation to the unit amount of N accumulated in legumes is quite low compared with that in cereals. Earlier studies showed that low productivity of legumes is a

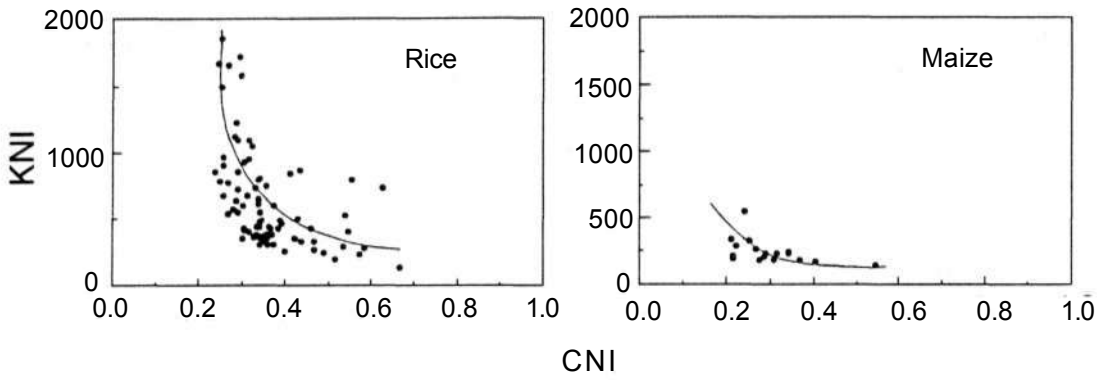


Fig. 11. Relationship between KNI and CN1 for rice and maize (after Osaki et al. 1996)

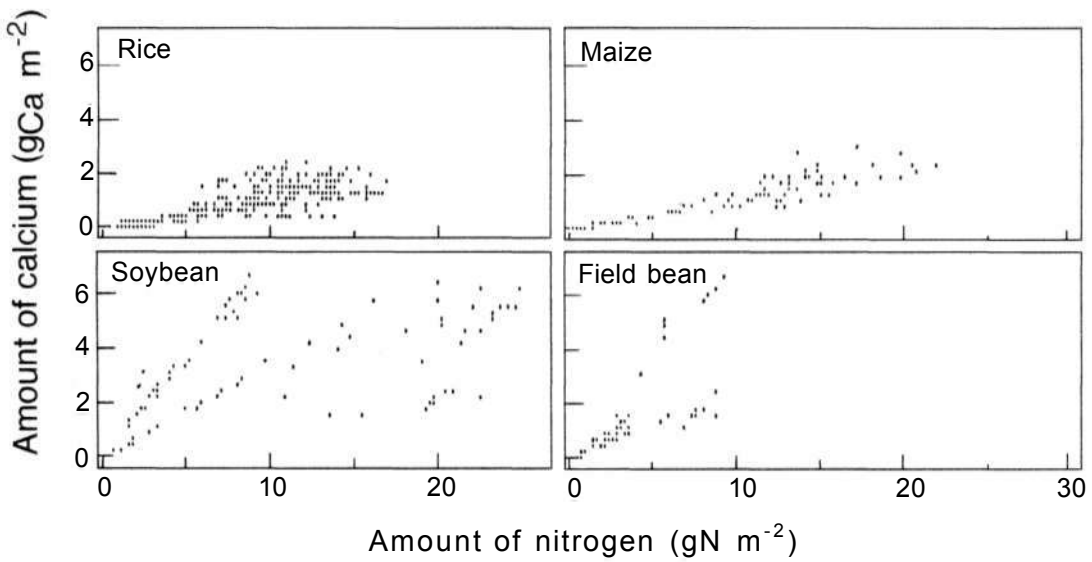
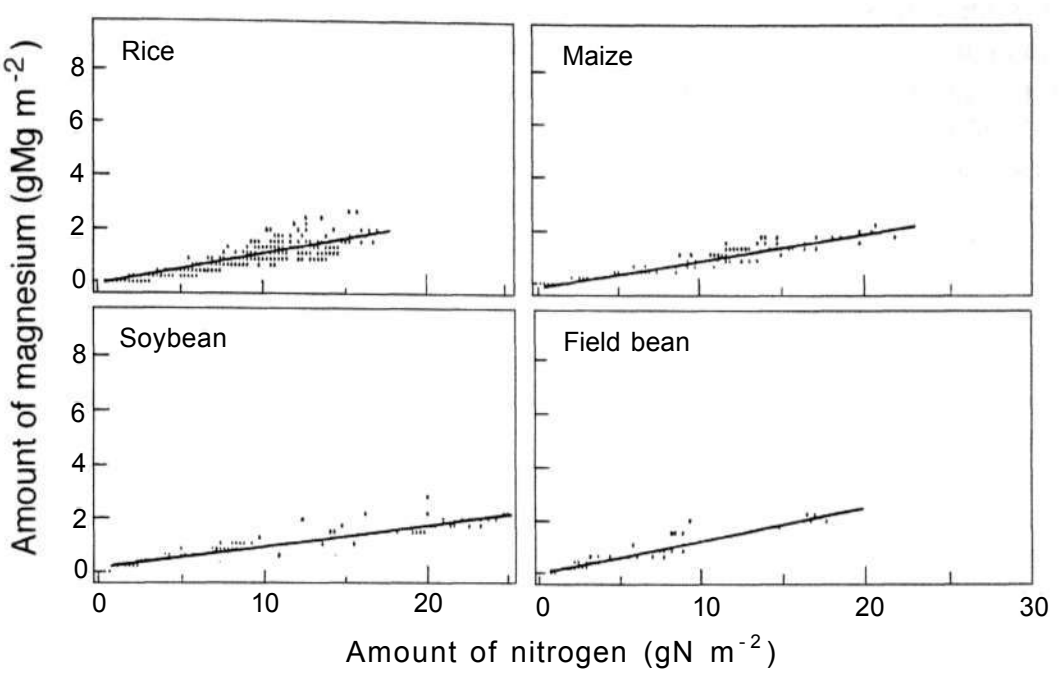


Fig. 12. Relationship between amount of Ca and amount of N accumulated at successive growth stages. Crops were grown with different rates of fertilizer application (modified from Osaki et al. 1996).

result of protein synthesis and N_2 fixation, for which a large amount of photosynthate is respired. However, our results presented here argues against this conclusion. Our results of the C-N interaction model, growth efficiency, and ^{14}C allocation show that triose-P produced by the Calvin cycle in legume leaves is dominantly distributed into pools of organic acids and amino acids compared with triose-P in cereal leaves. Our results of ^{14}C allocation support this hypothesis because photosynthates in leaves of legumes are distributed into organic acids and amino acids regardless of N-nutrition (Shinano et al. 1994 and Fig. 6). Moreover, ^{14}C respiration under light and dark in leaves of legumes is higher than that of cereals regardless of N-content. This basic difference in production



efficiency between cereals and legumes is not explained by the concept of growth and maintenance respiration. In addition, Yamaguchi (1978) reported that GE(DW) of harvested organs of rice and maize is 0.70 and that of soybean was 0.45, even though his data were not reproducible in our studies, in which GE(DW) of harvested organs of soybean was 0.77 (Shinano et al. 1993). Therefore, low productivity of legumes is not ascribed to synthesis of protein.

Accumulation of P, K, and Mg in legumes also linearly correlated with N-accumulation. In cereals, the interaction of C and N is affected by P-nutrition because if P is deficient, carbohydrate tends to distribute more into organic acids and amino acids owing to the acceleration in PEPC or PEP phosphatase activity (Champigny and Foyer 1992; Theodorou and Plaxton 1993) as shown in Figure 8. Thus, P-nutrition is also a factor that controls the C-.N interaction.

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